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# NORTH AFRICAN LOWER MIOCENE RHINOCEROSES

*By* W. R. HAMILTON


## SYNOPSIS

The Lower Miocene locality of Gebel Zelten is probably of the same age and part of the same faunal unit as Moghara, Siwa and Wadi Faregh, Egypt. It has yielded the remains of two rhinoceroses – *Aceratherium campbelli* sp. nov. and *Brachypotherium snowi* (Fourtau). Remains of these species are described and compared with the East African early Miocene rhinoceroses, which they resemble more closely than the European rhinoceroses. The amount of described material of *B. snowi* is greatly increased and our knowledge of the North African Lower Miocene *Aceratherium* is expanded.


## INTRODUCTION

THE discovery of fossil mammals at Gebel Zelten, Libya, was recorded by Arambourg and Magnier (1961) who collected in the area during 1960. Elements of the fauna were described in short notes by Arambourg (1961, 1961a, 1963). Collecting on a larger scale began in 1964 when Dr R. J. G. Savage first visited the area, and a preliminary note on this expedition (Savage & White 1965) contains a short faunal list which includes the rhinoceros *Brachypotherium*. Collecting in the area terminated in 1969. A large collection of fossil mammals from Gebel Zelten is now housed in Bristol University and at the British Museum (Natural History). Elements of the fauna described to date are – the ruminants (Hamilton 1973), *Megistotherium* (Savage 1973) and *Prodeinotherium* (Harris 1973). Studies of the anthracotheres, sirenians, gomphotheres, suids and carnivores are in preparation.

The geology of Gebel Zelten was described by Desio (1935), detailed sedimentological studies of the area were made by Selley (1966, 1967, 1969), and Doust (1968) studied the palaeoenvironment using invertebrate and trace fossils. The history of exploration, geography and geology of the area are summarized by Savage & Hamilton (1973).

The deposits at Gebel Zelten have been consistently dated as early Miocene by Arambourg (1961, 1961a, 1963), Savage (1967), Savage & White (1965) and Savage (in Selley 1969) refined the dating to early Lower Miocene. A faunal list for Gebel Zelten was given by Savage & Hamilton (1973). As Gebel Zelten and Moghara were probably part of the same faunal unit in early Miocene times, the faunal list for North Africa may be expanded by the inclusion of the Moghara, Siwa and Wadi Faregh faunas, resulting in a faunal list for the North African Lower Miocene sites which were probably also similar ecologically. The North African fauna agrees closely with the southern African sites, having three species in common with Muruarot (Madden 1972) and Rusinga (Bishop 1967); fairly close agreement with Bukwa (Walker 1969), and several genera in common with all three. Madden places

TABLE I

× agreement at specific level
○ agreement at generic level
a agreement at subfamily level

| | ZELTEN | MOGHARA | SIWA | WADI FAREGH | CONGO | S.W. AFRICA | BUKWA | RUSINGA | MURUAROT | NAPAK | SONGHOR |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Primates | | | | | | | | | | | |
| *Prohylobates tandyi* | | × | | | | | | | | | |
| Cetacea | | | | | | | | | | | |
| *Schizodelphis sulcatus* | | × | × | × | | | | | | | |
| *Delphinus vanzerelli* | | × | | | | | | | | | |
| *Sirenia* indet | × | | | | | | | | | | |
| Creodonta | | | | | | | | | | | |
| *Megistotherium osteothlastes* | × | | | | | | | ? | | | |
| *Anasinopa* sp. | ○ | | | | | | | ○ | ○ | | |
| *Hyainailouros fourtaui* | | × | | | | | | ○ | | ○ | |
| Carnivora | | | | | | | | | | | |
| *Afrocyon buroletti* | × | | | | | | | | | | |
| *Amphycyoninae* indet | a | | | | | | | a | | a | a |
| *Metailurus* sp. | ○ | | | | | | | ○ | | | ○ |
| Proboscidea | | | | | | | | | | | |
| *Gomphotherium spenceri* | | × | × | | | | | | | | |
| *G. angustidens* | × | × | | × | × | | ○ | × | × | × | ○ |
| *G. pygmaeus* | × | | | | | | | | | | |
| *Prodeinotherium hobleyi* | × | | | | × | | × | × | ○ | | |
| Hyracoidea | | | | | | | | | | | |
| Saghatheriinae | a | | | | | a | a | a | | | |
| Perissodactyla | | | | | | | | | | | |
| *Brachypotherium snowi* | × | × | × | | ○ | ○ | | ○ | ○ | ○ | |
| *Aceratherium campbelli* | × | × | | | ○ | | | ○ | ○ | ○ | |
| Artiodactyla | | | | | | | | | | | |
| *Brachyodus africanus* | | × | × | × | | | | | | | |
| *Brachyodus* sp. | ○ | | | | ○ | | ○ | ○ | ○ | ○ | |
| *Hyoboops africanus* | × | | | | | | ? | × | | | |
| *H. moneyi* | × | × | | | | | | | | | |
| *Masritherium depereti* | | × | | | | | | | | | |
| *Diamantohyus africanus* | × | | | | | × | × | | × | | |
| *Bunolistriodon massai* | × | | | | | | | ○ | ○ | | |
| *Bunolistriodon* sp. nov. | ○ | | | | | | | | | | |
| *Listriodon* sp. | ○ | | | | ○ | | ? | | | | |
| *Zarafa zelteni* | × | | | | | | | | ○ | | |
| *Prolibytherium magnieri* | × | | | | | | | | | | |
| *Dorcatherium libiensis* | × | | | | ○ | | ○ | ○ | | ○ | ○ |
| *Canthumeryx sirtensis* | × | | | | | | | | × | | |
| *Palaeomeryx* sp. | ○ | | | | | | ○ | ○ | | | |
| *Gazella* sp. | ○ | | | | | | | | | | |
| *Protragocerus* sp. | ○ | | | | | | | | | | |
| *Eotragus* sp. | ○ | | | | | | | | | | |

his Muruarot fauna in the early Miocene, using the figure of 18–22 million years given by Bishop, Miller & Fitch (1969) to define the limits of the lower Miocene in Africa. Napak is dated at 18–19 million years, Rusinga at about 19 million years, Songhor at 19·5–20 million years, and Bukwa at 22 million years (Bishop, Miller & Fitch 1969 p. 693). Bukwa (Mt Elgon) was independently dated at 22 million years by Brock & Macdonald (1969) and Rusinga at about 19·6 million years (VanCouvering & Miller 1969). Agreements at the specific and generic level between the North African faunas and the East African sites suggest that the North African sites may be aged between 19 and 22 million years.

Rhinoceroses were first described from the Lower Miocene of North Africa by Andrews (1900), who mentions an atlas vertebra which he assigns to an animal intermediate in size between *Aceratherium platyodon* and *Teleoceras* (= *Brachypotherium* here) *aurelianense*. Other specimens – an atlas and a scapula – were identified with *Aceratherium* sp. Fourtau (1918, 1920) described dental and post-cranial material from Moghara which he assigned to the new species *Teleoceras* (= *Brachypotherium*) *snowi*, and additional material which he identified with the *Aceratherium* sp. of Andrews (1900). The presence of *B. snowi* at Gebel Zelten was recorded on faunal lists by Arambourg & Magnier (1961) and Arambourg (1963), and *Aceratherium* featured on faunal lists by Savage (1967, and in Selley 1969). An isolated $M^3$ from Siwa, Egypt, was identified with *B. snowi* by Hamilton (1973).

Rhinoceroses are well represented in Miocene deposits from Africa south of the Sahara, and Hooijer (1966) describes and figures four genera from East Africa of which three – *Dicerorhinus leakyi*, *Aceratherium acutirostratum* and *Brachypotherium heinzelini* – are represented by a large amount of well-preserved material. *Aceratherium acutirostratum* was originally described by Deraniyagala (1951a, b) as *Turkanatherium acutirostratus*, and the genus *Turkanatherium* features in a faunal list by Savage (1956). The same specimen was redescribed and figured by Deraniyagala (1953). Arambourg (1959) suggested that *Turkanatherium* might be a synonym of *Aceratherium*; this was supported by Hooijer (1963, 1966, 1968). There is a large amount of isolated material from East Africa which is assigned to *A. acutirostratum*, but the type skull is in Ceylon and I have not been able to see this specimen.

*Dicerorhinus leakyi* was described by Hooijer (1966) on the basis of an almost complete skeleton and much isolated material, some of which is in the collections of the British Museum (Natural History). Deraniyagala (1965) established the species *Aceratherium leakyi* based upon material which Hooijer (1963) had assigned to other species and which he later (Hooijer 1967) reidentified when establishing that the name *Aceratherium leakyi* was invalid.

Three genera and species of rhinoceroses – *Brachypotherium heinzelini*, *Aceratherium acutirostratum* and *Aceratherium cf. tetradactylum* – were described from the Lower Miocene of the Congo (Hooijer 1963). The material of *B. heinzelini* includes an astragalus which is undoubtedly brachypothere in features and several cheek teeth of which a left $P^4$ is the type of the species. A large number of specimens from East Africa have increased the knowledge of this species, which was redescribed in much more detail by Hooijer (1966). An isolated left $M^2$ and a fragment of a right upper molar were identified as *Aceratherium cf. tetradactylum* by Hooijer (1963), but the $M^2$ was reidentified as *Brachypotherium heinzelini* (Hooijer 1966) and the fragment also presumably belongs with this species, thus the record of *A. cf. tetradactylum* from Africa is not valid.

Stromer (1926) records the presence of Rhinocerotidae indet. in the Lower Miocene, South West African fauna. The specimen consists of a mandibular fragment containing $P_4$ to $M_2$, but this was not figured by Stromer. This specimen was described by Heissig (1971), who identifies it as *Brachypotherium heinzelini*.

Hooijer (1966) identified an isolated $M^3$ from Loperot and two isolated upper molar fragments from Rusinga as *Chilotherium*. However, he later (Hooijer 1971) reidentified these specimens with the new genus *Chilotheridium*, which he described from numerous specimens including two skulls and much post-cranial material. The Loperot site and other sites containing *Chilotheridium* are of differing ages. The specimens from Rusinga may be of early Miocene age, but the sites yielding these specimens – Gumba and Wakondu – are not yet definitely dated. The Bukwa II locality which has yielded fragmentary remains of *Chilotheridium* is about 22 million years, but Kirimum, Loperot and Ngorora are of late Miocene and early Pliocene age.

To summarize ; the early Miocene records of rhinoceroses from Africa south of the Sahara indicate the presence of four genera and species – *Aceratherium acutirostratum*, *Dicerorhinus leakyi*, *Brachypotherium heinzelini* and *Chilotheridium* ; the last not being specifically identified by Hooijer (1971) from the sites of early Miocene age. In Lower Miocene deposits in North Africa two rhinoceroses are recorded – *Aceratherium* and *Brachypotherium snowi*. None of the African early Miocene rhinoceros species is known outside Africa.

The classification and identification of the European rhinoceroses are confused, and in the following work I have attempted to use forms which are well defined and described. I have made extensive use of the collection of European rhinoceroses housed in the British Museum (Natural History), and I tried to use the same comparative specimens as were used by Hooijer (1966). In this way cross-reference with Hooijer's work may be simplified.

## TERMINOLOGY

Anatomical terms used in this description are after Sisson & Grossman (1966) with the exception of the carpals and tarsals.

There is some controversy over the naming of the anterior teeth in rhinoceroses. The upper tusks are probably formed from the first upper incisors and this is generally accepted but the naming of the lower tusks is more difficult. Hooijer (1966) refers to these teeth as the canines but I have followed Radinsky (1969) who identifies them as the second incisors. In many forms, including at least one from Gebel Zelten, a pair of small incisors, probably the first, is present between the lower tusks.

Terms applied to the cheek teeth are after Osborn (1898) and Heissig (1969) and are demonstrated in text figure 1.

All the dimensions given in Tables 1–21 are measured in mm.

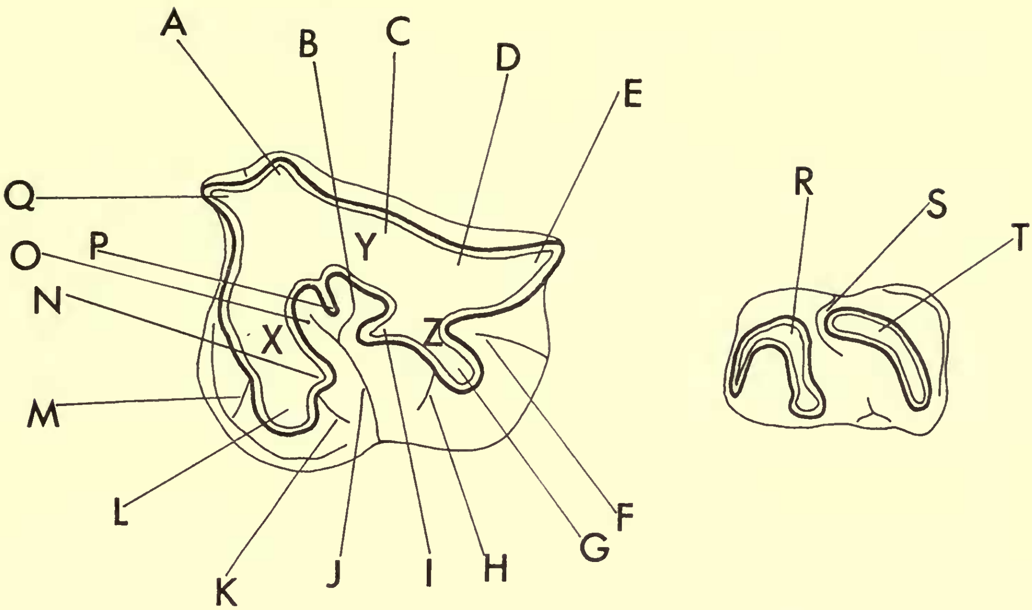


FIG. 1. Cusp nomenclature for the cheek teeth of rhinoceroses.
After Osborn (1898) and Heissig (1966).

A Paracone
B Medifossette
C Mesostyle
D Metacone
E Metastyle
F Postfossette
G Hypocone
H Hypocone groove
I Crochet
J Medisinus
K Posterior protocone groove
L Protocone
M Anterior protocone groove
N Antecrochet
O Prefossette
P Crista
Q Parastyle
R Metalophid
S Labial groove
T Hypolophid
X Protoloph
Y Ectoloph
Z Metaloph

## ABBREVIATIONS

Teeth are referred to by single capital letters – incisor (I), premolar (P), molar (M) and deciduous cheek tooth (D) – numbers are added above or below the line to define the tooth.

Specimens in institutions are referred to by: M., British Museum (Natural History), London; B.U., Department of Geology, University of Bristol; K.N., Centre for Prehistory and Palaeontology, Nairobi, Kenya. Recent material used was from the Department of Zoology, British Museum (Natural History) and is given the prefix M.O.

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gave permission for the reproduction of two colour slides as plates and Mr A. R. Lindsay donated specimen M.29251.

## SYSTEMATIC DESCRIPTIONS

### Genus *ACERATHERIUM* Kaup 1832

DIAGNOSIS. Large, usually hornless rhinoceroses; $I^1$ and $I_2$ developed as tusks; upper molars with strong antecrochet; crochet usually strong; protocone constricted by anterior and posterior grooves; limbs long; feet four-toed.

COMMENTS. Although a predominantly hornless group, Osborn (1899) states that rudimentary horns may be present on the frontals. The post-cranial skeleton is virtually indistinguishable from that of *Dicerorhinus*. Metacarpal V is usually well developed whereas in *Dicerorhinus* it is usually small (Hooijer 1966), but this feature is of little use in identifying other post-cranial elements.

### *Aceratherium campbelli* sp. nov.

DIAGNOSIS. A large species of *Aceratherium* in which the nasal notch is situated over $P^2$ and the facial region is long. The frontals are wide and a true sagittal crest is not developed. Supraoccipital region wide and vertical. Foramen ovale independent. Upper incisors well developed, $P^1$ large, cheek teeth high crowned. Length of cheek tooth row about 270 mm.

COMMENTS. This species is known only from North Africa, where it is well represented in the collections from Gebel Zelten and is also known from a few specimens from Moghara.

DERIVATION OF NAME. The trivial name is in honour of Dr A. Campbell of the Oasis Oil Company of Libya who provided much help and assistance during collecting expeditions to Gebel Zelten.

TYPE SPECIMEN. The skull (M.29250) which is almost complete but has poorly preserved cheek teeth (Pl. 1 & Pl. 2 fig. 3).

AGE AND LOCALITY. Lower Miocene. Gebel Zelten, Libya.

CRANIAL MATERIAL.

M.29250 : an adult skull in which the cheek teeth are poorly preserved and surface detail is difficult to see.
M.29251 : a pair of isolated nasals; donated by Mr A. R. Lindsay.
M.29252 : fragments of a shattered skull; cheek teeth; premaxillae and upper incisors.
M.29254 : a complete, isolated $M^3$.
M.29255 : a badly broken, isolated $M^3$ which agrees closely with M.29254.
M.29256 : the isolated lingual region of an $M^2$.
M.29257 : an isolated $P_4$ exhibiting medium wear.
M.29258 : an unerupted, isolated $M_3$.
M.29259 : a mandibular fragment with $P_2$–$M_1$ ($P_4$ only partly erupted) and fragments of $M_2$.
M.29266 : an isolated upper incisor which possibly belongs with *Aceratherium*.

M.29267 : labial fragments of $P^3$ and $P^4$, and the lingual region of $P^3$ : all from the uncollected skull (Pl. 3).

B.U.22925 : an almost complete left mandible with the posterior half of an unerupted $M_3$ and alveoli of $P_1$–$M_3$ preserved.

DESCRIPTION.

*The skull.* The sutures are completely closed on the skull (M.29250), and regions rather than individual bones are described. Much of the bone surface is coated with a ferrous concretion which is difficult or impossible to remove without seriously damaging the bone. The tips of the premaxillae, left wall of the cranium and crowns of most of the teeth are missing ; the nasals are broken off and their junction with the rest of the skull is not preserved. Isolated elements are used to amend the description and were identified by comparison with the skull wherever possible. M.29252 was a complete skull, but it was badly shattered during transport to England. The cheek teeth are broken and fragmented, preserved parts agree with those of M.29250 but are more lightly worn. The premaxillae and upper incisors are preserved (Pl. 4 fig. 1).

An almost complete rhinocerotid skull was discovered near Transportation Corner, Gebel Zelten (Savage & Hamilton 1973), by Dr R. C. Selley while he was carrying out sedimentological studies in the area. Selley photographed the skull and made brief notes but having no equipment suitable for the recovery of such a large specimen he was forced to leave it. The skull was not found again but tooth fragments M.29267 from site 15 (Savage & Hamilton 1973, text fig. 3) – field number 6415.16 – agree closely in size and state of wear with those photographed (Pl. 3) and a white concretion present on the labial fragments is similarly distributed on the labial faces of the photographed specimen. This agreement leaves little doubt that fragments M.29267 are from the skull which was presumably broken up for souvenirs by oil workers in the area. The skull is the best recorded from Gebel Zelten as the tooth rows are complete, fragments of associated lower jaws are preserved and the premaxillae are attached. Photographs of this skull are reproduced here (Pl. 3 figs. 1 & 2) as they are the only complete record of this specimen and they were used in the interpretation of the less complete material which was returned to England. The dimensions of the skull and its lateral profile agree closely with the skull M.29250, thus confirming the identification of this specimen.

*The skull : dorsal and facial regions.* The distal regions of the premaxillae are missing in M.29250 and are described from M.29252. The bone is flattened transversely with convex lateral and plane medial faces. The bone surface of the lateral region is smooth but the medial face is heavily sculptured with numerous nutrient foramina. The dorsal edge is sharp and the ventral edge flattened with a shallow pit lying behind the $I^1$ alveolus ; a similar pit is present on the skull (Pl. 3 fig. 1), in *A. incisivum* and in *D. schleiermacheri* a small $I^2$ is present in this region. The premaxilla becomes more flattened posteriorly, and the beginning of a ridge is preserved on the medial face of the left premaxilla. The proximal region of the premaxilla (M.29250) is shallow dorsoventrally, increasing in depth anteriorly and with a flattened medial region which reduces in width anteriorly. The bone curves ventrally and slightly laterally in front of the $P^1$ and is more slender but otherwise similar to that of *A. incisivum.* M.29250 and M.29252 have no regions of overlap, and the minimum length of the premaxillary region from the front of the $P^1$ was 130 mm; this agrees with measurements from Pl. 3 and compares favourably with *A. incisivum* in which it is 160 mm.

The facial region is longer than in *A. incisivum* and lacks the preorbital concavity. The nasal notch is anteriorly situated, lying above the anterior edge of $P^2$ (Pl. 1 fig. 3) as in *D. sumatrensis*; the notch is usually more posteriorly situated in aceratheres (Cooper 1934), lying over $M^1$ in *A. incisivum*, over $P^4$ in *A. tetradactylum* and *A. platyodon*, over $P^3$ in *A. lemanense* (Roman 1912 p. 63 fig. 19) and *A. acutirostratum* (Deraniyagala 1953 pl. 2 fig. b). The anterior border of the orbit is also anteriorly situated in M.29250, lying over the anterior end of $M^1$ whereas in *A. lemanense, A. platyodon, A. tetradactylum* and *A. acutirostratum* it lies over the anterior border of $M^2$, and in *A. incisivum* it lies over the middle of $M^2$.

The nasals of M.29250 are heavily encrusted and the bone surface is not visible; the isolated nasal M.29251 was used to amend this description. The nasals curve slightly dorsally from the face of the frontals as in *A. incisivum.* Owing partly to the more anterior position of the nasal notch, the lateral region of the nasals is stronger and deeper in the Zelten form than in *A. incisivum* but compares in depth with the nasals of *A. lemanense* (Roman 1912 pl. 8 fig. 1a). The surface of the bone is roughened distally, and nasals M.29251 carry roughening half-way along their dorsal surfaces, this region is also produced as a weak eminence (Pl. 2 figs. 1 & 2), which is similarly positioned to that in *Chilotheridium pattersoni.* However, the eminence is much weaker than that of *Chilotheridium* (Hooijer 1971 pls. 4 & 5), but it carries a similar median groove and could represent an incipient stage in the development of a *Chilotheridium* type of nasals. It is possible that a small nasal horn was developed in *A. campbelli,* and the eminence is certainly as strong as that on the frontals of *A. incisivum* which Osborn (1899) used as evidence for the presence of a frontal horn.

The nasals are relatively stout and the median face of each is a plane, unsculptured, vertical wall except at the tips and in the postero-ventral region, where heavy sculpturing suggests close joining of the bones. The nasals of *A. incisivum* are about the same length as those of *A. campbelli* but in the latter the tips are flexed whereas in *A. incisivum* this flexion does not occur.

The frontals are wide in the supraorbital region (Pl. 1 fig. 1) and the dorsal region of the skull is similar in shape to *A. lemanense* (Roman 1912 pl. 8 fig. 1). A true sagittal crest is not formed in M.29250 but the temporal crests approach each other very closely (Pl. 1 fig. 1); a similar crest is formed in *A. lemanense* and in one of the skulls of *A. incisivum* (Kaup 1834 pl. 10 fig. 2a). In the other skull of *A. incisivum* (Kaup 1834 pl. 10 fig. 2b) and in *A. acutirostratum* (Hooijer 1966, p. 137) the temporal crests do not approach so closely. In lateral aspect the dorsal face of the skull is very concave (Pl. 1 fig. 3) owing to the great height of the occipital region. The occipital region is also high in *A. tetradactylum* (Wang 1928 p. 188 fig. 1a) and rises steeply from the frontal region of the skull in *A. acutirostratum* (Deraniyagala 1953 pl. 2 fig. 2b). The skull of *A. incisivum* rises steeply but the profile is less saddle-shaped and the skull of *A. lemanense* is uniformly low.

The zygomatic arch is wide and deep with a strong notch near its posterior end in the area dorsal to the ear region. The ear region is exposed laterally between the lateral edge of the nuchal crest and a ridge from the posterior end of the zygomatic arch (Pl. 1 fig. 3) ; this lateral exposure is similar in *A. acutirostratum* but it is wider in *A. lemanense* and *A. incisivum*. M.29250 has a very strong nuchal crest which extends laterally forming a posterior wall for the temporal fossa ; this does not occur in *A. incisivum, A. lemanense* or *A. acutirostratum* in which the nuchal crests are much narrower.

*The skull : occipital and basicranial regions.* The supraoccipital region is vertical in M.29250 as is usual in the aceratheres (Cooper 1934 p. 572). The dorsal region of the nuchal crest is not reflected, in contrast to *A. incisivum* and *A. lemanense* but in agreement with *A. acutirostratum*. Also in agreement with this species the occipital condyles are produced posteriorly to a greater extent than in *A. incisivum* or *A. lemanense*. The condyles are relatively large in M.29250 and in *A. acutirostratum* but are smaller in *A. incisivum* and *A. lemanense*.

In posterior aspect (Pl. 2 fig. 3) the occipital region differs in shape from the other aceratheres, mainly due to the great expansion of the nuchal crests. The supraoccipital region bears a deep median depression with a large tubercle and paired lateral depressions which are clearly defined by strong ridges above the condyles (Pl. 2 fig. 3). Unfortunately this region cannot be compared with that of *A. acutirostratum*, as the type skull of this species has undergone lateral compression and distortion. Ventrally the nuchal crest joins the post-tympanic process anterolateral to the condyles and from this the paroccipital process is produced : neither process is preserved but their bases suggest that the processes were relatively weak.

The basioccipital region is badly broken and is largely missing from M.29250 (Pl. 1 fig. 2). An anterior process was developed for the attachment of the rectus capitis ventralis muscle, and the post-tympanic process approaches the postglenoid process, but these regions do not fuse. The hypoglossal foramen is more anteriorly situated than in *R. unicornis, D. sumatrensis* or *A. incisivum* lying antero-medial to the base of the paroccipital process. The auditory region is exposed ventrally (Pl. 1 fig. 2) near the medial end of the paroccipital process and medial to it are two large foramina; one is probably the posterior lacerate foramen, and the lateral one is the stylomastoid foramen. Further details of the auditory region are obscured. The median lacerate foramen lies anterior to the auditory region. An important feature of the skull is the independent existence of the foramen ovale which lies anterior to the median lacerate foramen and slopes posterodorsally from its opening. The latter foramen is joined to the alisphenoid canal by a shallow groove, and a groove for an artery runs from its ventral edge into the ear region. The existence of an independent foramen ovale is unusual in rhinoceroses as the foramen lacerum medius and the foramen ovale are usually fused. However, Osborn (1898), with particular reference to the North American rhinoceroses, states that all degrees of fusion of the two foramina are demonstrated by the Oligocene and Miocene rhinoceroses, and an independent foramen ovale is known from *Chilotherium* (Edinger 1937 ; Edinger & Kitts 1954), though this is more posteriorly

TABLE 2

The skull of *Aceratherium campbelli*

| | *Aceratherium campbelli* | *A. incisivum* | *A. acutirostratum*[1] | *A. lemanense*[2] | *Dicerorhinus leakyi*[3] |
|---|---|---|---|---|---|
| Length of skull. Occipital crest–tips of nasals | *c* 560–580 | 531 | 586 | 510 | 630 |
| Width across postorbital processes | *c* 176 | 185 | 156 | – | – |
| Maximum height of occiput | 239 | 228 | 157 | – | – |
| Depth of naso-maxillary notch from tip of premaxilla | – | 270 | – | – | 145 |
| Facial length from naso-maxillary notch to anterior edge of orbit | 110 | 78 | 109 | – | 135 |
| Length from front of orbit to posterior face of occipital condyles | 355 | 389 | 329 | – | – |
| Depth of skull and teeth at anterior edge of orbit | *c* 196 | 211 | 207 | – | – |
| Width across zygomatic arches | 380 | 345 | 320 | – | – |
| Maximum width of occipital region | 278 | 263 | – | – | – |

[1] After Deraniyagala 1951. [2] After Roman 1912. [3] After Hooijer 1966.

situated. The optic foramen opens immediately above the $M^2$. Between the foramen ovale and the optic foramen the bone is badly shattered, but the posterior opening of the alisphenoid canal is preserved and the foramen rotundum presumably opened into this canal.

In general features the skull of *A. campbelli* resembles that of *A. acutirostratum* more closely than any other acerathere, but it must be emphasized that this comparison and apparent resemblance are based upon published plates only. The anterior position of the orbit and nasal notch, form of the frontals, basicranial region and occiput serve to distinguish the skull of *A. campbelli* from that of *A. acutirostratum.*

*Mandible.* A nearly complete mandible of an almost adult individual (B.U.22025) is identified with *A. campbelli.* It is slightly smaller than those identified with *B. snowi* and the length of the cheek tooth row is about 240 mm which would rise to 250 mm in the fully adult condition ; this compares with an estimated length of 300 mm on mandible M.25126 which is identified with *B. snowi.* The mandible is shallow and similar in shape to that of *A. incisivum,* the ventral edge is slightly convex, and the leading edge of the vertical ramus rises steeply from the region of the partially erupted $M_3$ ; this leading edge is convex and relatively narrow. There are paired mental foramina with the larger lying below $P_1$. The symphysis starts in front of $P_1$ and was probably relatively short. The root of $I_2$ terminates in front of the $P_1$ in B.U.22025 and also in M.29259. The posterior half of the partially erupted $M_3$ is preserved ; this fragment indicates the presence of a strong labial groove which is a feature of the acerathere lower cheek teeth (Hooijer 1966), rather than of brachypothere teeth.

*Upper dentition.* The upper incisors of M.29252 are preserved (Pl. 4 fig. 1) ; they are almost complete and heavily worn. Hooijer (1966, p. 142) used the ratio of antero-posterior crown diameter to root length as a possible criterion by which the incisors of *Aceratherium* could be distinguished from those of *Brachypotherium.* On the $I^1$ of *Brachypotherium goldfussi* (Kaup 1854 : pl. 1 fig. 13) the antero-posterior crown diameter is greater than the root length, and in the $I^1$ of *B. brachypus* (M.33524) the crown length is 86 mm and the root length is not greater than 80 mm. This contrasts with the condition in the upper incisors of *A. incisivum* (Kaup 1834 pl. 14 figs. 1–3) in which the root length is always much greater than the crown length. The right upper incisor of M.29252 is the more complete and its root length exceeds the antero-posterior diameter of the crown (Table 3), which helps to confirm the identification of M.29252 as *Aceratherium* if Hooijer's criteria are valid. The crown of the incisor is heavily worn posteriorly but the anterior region is unworn (Pl. 4 fig. 1) ; this agrees with the wear pattern in *A. incisivum,* but differs from the wear in *D. sumatrensis* and *D. schleiermacheri* in which the whole crown of the tooth is worn uniformly.

An isolated, unerupted, right $I^1$ (M.29266) is smaller than those of M.29252. It has a long root (Pl. 4 fig. 6), and therefore cannot be identified with *Brachypotherium.* The tooth agrees closely with that of *A. incisivum* figured by Kaup (1834 pl. 14 fig. 7), but also agrees closely with that of *D. leakyi* (Hooijer 1966 pl. 4 fig. 7). The incisors of *A. incisivum* exhibit considerable variation in size and only a single individual of *A. campbelli* is represented by M.29252. M.29266 may thus simply represent a smaller individual of *A. campbelli*, or it may possibly indicate the presence of *Dicerorhinus* at Gebel Zelten.

*Dentition : upper cheek teeth.* The isolated upper cheek teeth and shattered upper dentitions of *Aceratherium* from Gebel Zelten have few corresponding parts preserved. This is unfortunate as it introduces some uncertainty into the grouping of these specimens. However, comparison of the material demonstrates that all the teeth fall into the same size range (Table 3), and features of the teeth are similar within the degree of variation usual in the rhinoceroses. The skull (M.29252) has a few upper teeth preserved and wherever possible these are used in the description to confirm the identification of isolated teeth.

A complete $M^3$ (M.29254) presents features characteristic of *Aceratherium.* The anterior cingulum is strong, giving way labially to a vertical depression on the face of the parastyle. The protocone constriction is strong with anterior and posterior grooves similar to *A. incisivum* and *A. lemanense,* but contrasting with *Dicerorhinus* in which the grooves are not present and the constriction consists of an anterior depression only. A hypocone groove is not present on either of the upper third molars. Immediately labial to the posterior protocone groove the antecrochet bulges basally extending across the medisinus ; this contrasts with *Dicerorhinus* (Hooijer 1966 p. 139). The parastyle is strong and narrow antero-posteriorly. The paracone swelling is very feeble, increasing in strength basally but is much weaker than in *D. leakyi, D. sumatrensis, A. incisivum* or *A. lemanense* ; as a result the posterior face of the tooth is convex (Pl. 4 fig. 3) whereas in the other species it carries a shallow labial concavity. The crochet is strong (Pl. 4 fig. 5), reducing basally. The presence of a crochet in M.29255 is indicated by a fold of the enamel face in the medisinus ; a crochet is present in *A. incisivum, A. lemanense* and *A. acutirostratum.* The medisinus is wide lingually (Pl. 4 fig. 3), and lacks a tubercle at its lingual end. A small postero-lingual cingulum is present and a weak posterior cingulum ; lingual cingula are present in *A. lemanense* and *A. incisivum* but their presence and strength are variable.

The lingual region of the $M^1$ has a strong anterior cingulum as in the $M^3$ ; the protocone is strongly constricted in M.29252 (Pl. 5 fig. 1), on the skull (M.29250 : Pl. 1 fig. 2), on the uncollected skull (Pl. 3), and on the $M^2$ fragment (M.29256 : Pl. 4 fig. 2). This is as in *A. lemanense, A. incisivum* and *A. acutirostratum,* but is in contrast to *Dicerorhinus.* A weak hypocone groove is also present on M.29252 and M.29256 as is usual when the protocone is strongly constricted (Hooijer 1968), but in contrast to the $M^3$. The antecrochet increases in strength basally, extending across the medisinus as in the $M^3$ and the other aceratheres, but in contrast to *Dicerorhinus.* The crochet is strong as in the $M^3$ but is more labially situated and is flexed more labially. The medisinus is open as in the $M^3$ and lacks a tubercle at the lingual end in M.29256 and M.29250 ; this region is not preserved in M.29252. The postero-lingual cingulum is strong and continues with the postfossette, but there is no extension of either posterior or anterior cingula onto the lingual region of the tooth ; this contrasts with *A. incisivum* and *A. lemanense* in which the cingula may extend onto the lingual face but do not usually join lingually. The labial region of $M^1$ is preserved on M.29252 ; the parastyle is weaker and the paracone relatively stronger than in *A. lemanense* (M.29264) as a result the antero-labial corner of the $M^1$ slopes more sharply lingually than is usual in the aceratheres. The labial face is shallowly concave and smoothly curved with a weak postero-labial cingulum and the posterior corner is sharp.

The $P^4$ (M.29252 : Pl. 5 fig. 1) exhibits medium wear and is almost complete ; a very heavily worn but nearly complete $P^4$ is preserved on the skull (M.29250 : Pl. 1 fig. 2) and the labial face of the $P^4$ (M.29267) is preserved from the uncollected skull (Pl. 3) ; this demonstrates that the tooth was very high. $P^4$ has a weaker protocone constriction than on the molars and the anterior protocone groove is weak (Pl. 5 fig. 1) ; this is also the case in *A. lemanense* and *A. incisivum.* The antecrochet is strong, extending across the medisinus and joining the base of the metaloph in M.29252 and probably also in M.29250. A crista is not present, but a swelling at the base of the medisinus in M.29252 suggests the presence of a crochet. The medisinus is narrow and a wide tubercle crosses the lingual opening. A strong cingulum is present in *A. lemanense* but in *A. incisivum* the condition is similar to the Zelten form, with a strong antero-posterior tubercle in the opening of the medisinus. The labial face of the $P^4$ is very high in M.29267 and shallowly concave as in *A. incisivum,* but in contrast to *A. lemanense* in which the face is slightly convex owing to the weakness of the paracone rib. This rib is very strong in M.29252 and in M.29267 but is not preserved in M.29250. A labial cingulum is not present in M.29252, M.29250, M.29267, *A. incisivum* or *A. lemanense,* but the anterior and posterior cingula are strong.

The lingual and labial regions of the right $P^3$ and the lingual region of the left $P^3$ are preserved on M.29252, and the almost complete left and right third premolars are preserved on M.29250. Unfortunately the latter specimens are heavily worn and the crowns are broken and obscured by matrix. The labial and lingual regions of the $P^3$ are also preserved (M.29267) from the uncollected skull ; these parts cannot be joined but almost the complete tooth is preserved. The protocone constriction is nearly lost as in *A. incisivum.* The antecrochet extends across the medisinus as in the $P^4$ and the molars, but it is weaker than in *A. lemanense* or *A. incisivum.* A crochet was probably present as indicated by a swelling of the anterior face of the metaloph on M.29267 and the left $P^3$ of M.29252. The labial face of the tooth is shallowly convex with a weak central swelling, and the paracone rib is much weaker than in the $P^4$ ; this is also true of *A. lemanense* but may be partly a wear factor. The anterior and posterior cingula are strong, and there is a strong tubercle at the lingual opening of the medifossette as in the $P^4$.

$P^2$ is preserved on the left side of M.29252 and on both sides of M.29250. It has a wide ectoloph and a relatively short protoloph and metaloph as in *A. incisivum* and *A. lemanense.* Strong anterior and posterior cingula are present, and the tubercle in the medisinus extends anteriorly almost joining the anterior cingulum ; in *A. lemanense* the lingual cingulum is very strong, but in *A. incisivum* it is weaker and similar to that of M.29252.

The dentitions of *Aceratherium* from Gebel Zelten agree with those of *A. lemanense* and *A. incisivum,* but are distinct from both. From published descriptions and figures of *A. acutirostratum* (Deraniyagala 1951a, 1953 ; Hooijer 1963, 1966), the

TABLE 3

The upper dentition of *Aceratherium campbelli*

| | M.29252 | | M.29266 | M.29250 | | M.29255 | M.29267 | *A. acutirostratum* Congo | *A. acutirostratum* E. Africa | *A. incisivum* | *D. leakyi* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *r.* | *l.* | | *r.* | *l.* | | | | | | |
| $I^1$ | | | | | | | | | | | |
| Antero-posterior length | 46 | 46 | 37 | – | – | – | – | – | – | 48 | 38 |
| Transverse width | 18 | 19 | 15 | – | – | – | – | – | – | 17 | 18 |
| Total length | 70 | 71 | 57 | – | – | – | – | – | – | 95 | – |
| $P^1$ | | | | | | | | | | | |
| Antero-posterior length | 23 | 24 | – | 22 | 24 | – | – | – | – | 25 | – |
| Maximum transverse width | 20 | 21 | – | 20 | 21 | – | – | – | – | 20 | – |
| $P^2$ | | | | | | | | | | | |
| Antero-posterior length | 30 | 31 | – | 29 | *c* 28 | – | – | 32 | – | 32 | 26 |
| Anterior transverse width | 30 | – | – | *c* 34 | – | – | – | – | – | 40 | 34 |
| Posterior transverse width | 37 | – | – | *c* 37 | – | – | – | – | – | 44 | 36 |
| $P^3$ | | | | | | | | | | | |
| Antero-posterior length | – | 42 | – | 35 | 35 | – | *c* 36 | – | 32 | 35 | 29 |
| Anterior transverse width | – | – | – | 49 | 48 | – | – | – | 46 | 54 | 43 |
| Posterior transverse width | – | 48 | – | – | 49 | – | – | – | 42 | 53 | 44 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| $P^4$ | | | | | | | | | | | |
| Antero-posterior length | – | 47 | – | 45 | – | – | 45 | 46 | – | 37 | 31 |
| Anterior transverse width | – | 62 | – | c 60 | – | – | – | 60 | – | 59 | 51 |
| Posterior transverse width | – | 56 | – | 55 | – | – | – | 53 | 46 | 55 | 49 |
| $M^1$ | | | | | | | | | | | |
| Antero-posterior length | – | 51 | – | c 47 | – | – | – | – | 52 | 42 | 36 |
| Anterior transverse width | – | 68 | – | c 64 | – | – | – | – | 62 | 54 | 50 |
| Posterior transverse width | – | – | – | – | – | – | – | – | 56 | 48 | 46 |
| $M^2$ | | | | | | | | | | | |
| Antero-posterior length | – | – | – | c 50 | – | – | – | – | 56 | 43 | 41 |
| Anterior transverse width | – | – | – | – | – | – | – | – | 64 | 58 | 55 |
| Posterior transverse width | – | – | – | – | – | – | – | – | 57 | 59 | 46 |
| $M^3$ | | | M.29254 | | | | | | | | |
| Antero-posterior length | – | – | 47 | – | – | c 47 | – | – | 57 | 45 | 42 |
| Anterior transverse width | – | – | 49 | – | – | 49 | – | – | 62 | 51 | 51 |
| Length of outer face | – | – | 55 | – | – | 54 | – | – | 65 | 59 | 52 |
| Length of molar row | – | – | – | – | c 150 | – | – | – | c 154 | 130 | – |
| Total length of tooth row | – | – | – | – | 270 | – | – | – | – | 260 | – |

agreement is closer than with the European species, which supports similarities of the skull.

*Lower dentition.* Lower incisors are not known, but their presence is indicated by the mandibles (M.29259 & B.U.22025). If the identification of these specimens with *Aceratherium* is correct, then this animal had short rooted incisors, the root ending anterior to the $P_1$.

*Lower dentition : cheek teeth.* Mandible B.U.22025 contains the alveoli of the cheek teeth ; two isolated cheek teeth M.29254 and M.29257 are also identified with *Aceratherium.* The latter is lightly worn and is probably a $P_4$, while the former is unerupted and is probably an $M_3$. A mandibular fragment (M.29259) – with $P_2$ and $P_3$ erupted, a partially erupted $P_4$, an almost complete and erupted $M_1$ and fragments of $M_2$ – is also identified with *Aceratherium.* These specimens all agree closely with the cheek teeth of *Aceratherium incisivum* (M.375) ; they carry strong labial grooves and are relatively wide.

The lightly worn $P_3$ (Pl. 7 figs. 1, 2) is almost fully molariform, with well-developed metalophid and hypolophid ; the labial groove is strong (Pl. 7 fig. 2) and extends to the base of the crown. The anterior lingual valley is shallower than the posterior and swells lingually well above the base of the crown ; as a result the anterior valley is lost after medium wear, a feature in which the tooth resembles *D. sumatrensis.* The tooth also resembles *A. incisivum* and *D. leakyi* (M.18921).

The $P_4$ is not fully erupted in M.29259 but M.29257 (Pl. 4 fig. 5) agrees closely with this tooth and is probably also a $P_4$. The tooth is fully molariform and relatively wide ; the anterior valley is again shallower than the posterior and would be lost first in wear. The labial groove is very deep in both specimens.

Each molar carries a deep labial groove (Pl. 7 fig. 2 & Pl. 4 fig. 4) and a lingual cingulum is present in the anterior region of M.29254 (Pl. 4 fig. 4). The molars are low crowned and may be distinguished from those of *Brachypotherium* on this basis as well as the strength of the labial groove.

*Cranial and dental features of A. campbelli : a summary.*

The upper dentition of the Zelten form is characteristically acerathere in main features. The presence of a strong protocone constriction, especially on the two more anterior molars, the narrow lingual entrance of the medisinus, the strength of the antecrochet and the flatness of the ectoloph serve to distinguish this dentition from that of *D. leakyi,* and at the same time to ally it with *A. acutirostratum.*

The cranial features are difficult to interpret. The eye is low on the skull and anteriorly situated ; the facial region is long and the nasal notch more anterior than in *A. acutirostratum,* though more posterior than in *D. leakyi* (Hooijer 1966 pl. 1). A frontal eminence and presumably a frontal horn were not present, but a small nasal horn was probably present as indicated by the weak nasal eminence and rugosity of the bone surface in this region. Frontal and very strong nasal eminences are present in *D. leakyi* but neither are present in *A. acutirostratum.* The temporal crests, occipital crests, nasals, supraoccipital region and basicranial regions differ widely in *A. campbelli* and *A. acutirostratum.*

TABLE 4

Lower dentition of *Aceratherium campbelli*

| | M.29259 | M.29257 | M.29258 | *A. acutirostratum* | *A. incisivum* | *D. leakyi* | *A. lemanense* |
|---|---|---|---|---|---|---|---|
| $P_1$ | | | | | | | |
| Antero-posterior length | 4 root | – | – | – | – | 18 | – |
| Width | 5 only | – | – | – | – | 11 | – |
| $P_2$ | | | | | | | |
| Antero-posterior length | 27 | – | – | – | 26 | 26 | – |
| Anterior transverse width | 14 | – | – | – | 19 | 16 | – |
| Posterior transverse width | 17 | – | – | – | 23 | 17 | – |
| $P_3$ | | | | | | | |
| Antero-posterior length | 32 | – | – | 36 | 35 | 31 | – |
| Anterior transverse width | 22 | – | – | 20 | 24 | 21 | – |
| Posterior transverse width | 26 | – | – | 22 | 29 | 23 | – |
| $P_4$ | | | | | | | |
| Antero-posterior length | *c* 32 | 35 | – | – | 37 | 35 | 35 |
| Anterior transverse width | *c* 23 | 26 | – | 25 | 31 | 26 | 26 |
| Posterior transverse width | *c* 28 | 28 | – | 26 | 31 | 28 | 28 |
| $M_1$ | | | | | | | |
| Antero-posterior length | 40 | – | – | – | 43 | – | 42 |
| Anterior transverse width | 30 | – | – | 26 | 35 | 29 | 36 |
| Posterior transverse width | 31 | – | – | 29 | 36 | 30 | 35 |
| $M_2$ | | | | | | | |
| Antero-posterior length | – | – | – | 48 | 45 | 41 | 52 |
| Anterior transverse width | – | – | – | 30 | 35 | 32 | 35 |
| Posterior transverse width | – | – | – | 31 | 35 | 31 | 35 |
| $M_3$ | | | | | | | |
| Antero-posterior length | – | – | 46 | 53 | 43 | 44 | 53 |
| Anterior transverse width | – | – | 28 | 30 | 32 | 30 | 35 |
| Posterior transverse width | – | – | 27 | 29 | 30 | 28 | 34 |

The only other early Miocene rhinoceros from Africa with which this species could be confused is *Chilotheridium*, which occurs in the Bukwa fauna (Hooijer 1971, and probably those identified as *Chilotherium*, Walker 1968, 1969). However, the chances of confusion here are very slight as *Chilotheridium* has higher cheek teeth in which the antecrochet is very strong and curves basally towards the entrance of the medisinus, a feature which does not occur in *A. campbelli*.

*Post-cranial.* The post-cranial material identified with the long-limbed rhinoceroses is more abundant than that identified with *Brachypotherium*. It all appears to belong to the same genus which is probably *Aceratherium*.

Post-Cranial Material.

M.29284 : proximal fragment of a right Mc.III.
B.U.22031 : proximal fragment of a right Mt.III.
B.U.22032 : distal end of a Mt.III.
M.29287 : right astragalus.
B.U.22034 : right astragalus.
M.29289 : left astragalus.
B.U.22036 : left astragalus.
B.U.22037 : almost complete, right Mt.IV.
B.U.22038 : proximal region of a right Mt.II.
B.U.22039 : proximal region of a left Mt.III.
B.U.22040 : almost complete, right Mt.IV.
B.U.22041 : almost complete, right Mc.IV.
B.U.22042 : complete, right Mc.II.
B.U.22043 : phalange I of a posterior median digit.
B.U.22044 : lateral hind first phalange.
B.U.22045 : lateral hind first phalange.
B.U.22046 : lateral hind first phalange.
B.U.22047 : lateral hind first phalange.
B.U.22048 : phalange II of a median digit.
B.U.22049 : lateral hind first phalange.

Description.

*Metacarpals.* A right Mc.II (B.U.22042) is complete but the distal end is slightly eroded. The bone is long, slender (Table 5) and almost straight (Pl. 5 fig. 2). Its distal end is narrow with a weak posterior keel. The bone surface is smooth anteriorly, but the posterior face exhibits some roughening of the surface, partly sculpturing and partly due to erosion. The proximal end of the bone is very flattened transversely and is triangular; the medial and lateral faces are slightly concave proximally. The proximal facet is convex antero-posteriorly and transversely; a lateral facet is not visible but may have been eroded away. On the Mc.II of the East African long-limbed rhinoceroses (M.18842 : Hooijer 1966 pl. 12 fig. 4) the lateral face carries an antero-posteriorly elongate facet which faces laterally, and articulates partly with the medial facet of the Mc.III and partly with the medio-distal facet of the magnum. In *R. unicornis* (M.O.1961.5.10.1) the lateral facet of the Mc.II is sharply divided into a large facet facing medio-proximally and a small anterior facet facing disto-medially ; the latter articulates with a small facet on the Mc.III. The lateral facets are similar to this in *D. sumatrensis* (M.O.1949.1.11.1), but the anterior facet is much larger. This anterior facet is absent in the Mc.II from Gebel Zelten (M.29300), and the corresponding facet in the Mc.III is also absent.

A proximal fragment of the right Mc.III (M.29284) is much narrower than the Mc.III of the short-limbed form (M.29275) and the medial proximal facet is narrower and more deeply concave. The bone is swollen in the proximo-medial corner of the anterior face but the swelling is far smaller than the large tuberosity which is developed in the Mc.III of the short-limbed form. The Gebel Zelten Mc.III fragment agrees closely with an Mc.III from East Africa (M.18841 : Hooijer 1966 pl. 12 figs. 2, 3), and with that of *D. schleiermacheri* (M.1281) from Eppelsheim. The medial facet is similar in size, shape and concavity and the lateral facet is also similar.

A right Mc.IV (B.U.22041) is badly eroded proximally and shattered distally, with a fragment missing from the lateral face half-way along the shaft, and with only the lateral distal region preserved. The bone is strongly curved laterally (Pl. 5 fig. 5), as in the fourth metacarpals from East Africa (M.18814 : Hooijer 1966 pl. 12 fig. 3 & M.18811 : Hooijer 1966 pl. 12 fig. 1). However, the Gebel Zelten specimen is more slender (Table 5) than the East African specimens. The proximal facet is triangular and transversely concave ; it is much narrower than that of M.18814 from East Africa, and its medial facets are smaller in agreement with the lateral facets of the Mc.III, which are also small.

There can be little doubt that these metacarpals belong to the same species ; they indicate a long-limbed, highly cursorial animal in which the Mc.III was dominant and the side-toes were reduced further than in the East African long-limbed rhinoceroses. It is unfortunate that a complete Mc.III is not known, but its length can be estimated from the lengths of the Mc.II and the Mc.IV and must have approached that of *D. schleirmacheri*, lying in the region 180–200 mm.

*Astragalus*. Four almost complete astragali – M.29287, M.29289, B.U.22036 and B.U.22034 – and several fragments are identified with the long-limbed rhinoceroses and agree closely in anatomy with the astragalus of *D. sumatrensis* (M.O. 1949.1.11.1), with astragali from Europe of *A. incisivum* (M.1290 : Kaup 1834 pl. 15 fig. 2) and with those from East Africa (listed Hooijer 1966 : Table 42). The astragali from Gebel Zelten show variation in size and anatomical details such as size of facets, but in all cases the median height is similar to the width, and the ratio of the median height to total width is higher than in the short-limbed form (Tables 6 and 13).

*Metatarsals*. The proximal ends of left and right second metatarsals (B.U.22039 & B.U.22038) are preserved ; the latter is more complete with about three-quarters of the shaft preserved. The bone is strongly curved medially as in *R. unicornis* and *D. sumatrensis* ; it is long and slender with transversely convex anterior and concave posterior faces. The lateral face is plane where it rests against Mt.III. The proximal facet is transversely concave and antero-posteriorly convex ; it is sub-triangular in shape. An elongate, single lateral facet is present on B.U.22038, but on B.U.22039 paired anterior and posterior facets are present ; these articulate with the Mt.III and the disto-medial facets of the cuneiform. In *R. unicornis*

TABLE 5

*Aceratherium* : Metacarpals

| | Mc.II | | Mc.III | | Mc.IV | |
|---|---|---|---|---|---|---|
| | B.U.22042 | E. Africa M.18843 | M.29284 | E. Africa M.18837 | B.U.22041 | E. Africa M.18814 |
| Length | 142 | – | – | – | 142 | 150 |
| Proximal width | 23 | 43 | 62 | 49 | 37 | 51 |
| Proximal antero-posterior depth | 36 | 47 | 47 | 38 | 35 | 47 |
| Middle width | 22 | 38 | – | 43 | 24 | 35 |
| Middle antero-posterior depth | 21 | – | – | 18 | 17 | 22 |
| Distal width | 28 | – | – | – | – | 50 |
| Distal antero-posterior depth | 24 | – | – | – | 30 | 41 |
| Width of distal trochlea | 28 | – | – | – | – | 44 |

TABLE 6

*Aceratherium* : Astragalus

| | M.29289 | M.29287 | B.U.22034 | E. African forms M.18881 | E. African forms M.18875 | *D. schleiermacheri* M.2786 | *A. incisivum* M.2755 | *D. sumatrensis* |
|---|---|---|---|---|---|---|---|---|
| Lateral height | 61 | *c* 65 | *c* 73 | 67 | 66 | 79 | 79 | 67 |
| Median height | 60 | 67 | 71 | 65 | 68 | 74 | 67 | 66 |
| Total width | 57 | 77 | – | 82 | 73 | 94 | 86 | 69 |
| Ratio median height/total width | 1·05 | 0·87 | – | 0·79 | 0·93 | 0·78 | 0·78 | 0·97 |
| Trochlea width | 59 | 63 | – | 65 | 64 | 79 | 78 | 67 |
| Width of distal facets | 64 | 64 | – | 73 | 68 | 76 | 68 | 66 |

TABLE 7

*Aceratherium* : Metatarsals

| | Mt.II | | | Mt.III | | | Mt.IV | | |
|---|---|---|---|---|---|---|---|---|---|
| | B.U.22039 | B.U.22038 | E. Africa | B.U.22031 | B.U.22032 | E. Africa | B.U.22037 | B.U.22040 | E. Africa |
| Length | – | – | 162 | – | – | 180 | 151 | 165 | 160 |
| Proximal width | 30 | 29 | 29 | 55 | – | 57 | 47 | 41 | 44 |
| Proximal antero-posterior depth | 48 | 49 | 48 | 42 | – | 49 | 44 | 38 | 46 |
| Middle width | 29 | 34 | 32 | 51 | – | 50 | 27 | 28 | 29 |
| Middle antero-posterior depth | 29 | 20 | 30 | 25 | – | 25 | 25 | 23 | – |
| Distal width | – | – | 42 | – | 64 | 60 | 36 | 34 | 38 |
| Distal antero-posterior depth | – | – | 41 | – | 43 | 41 | 34 | 33 | 40 |
| Width of distal trochlea | – | – | 36 | – | 54 | 51 | 30 | 31 | 37 |

(M.O.1961.5.10.1) paired facets are present in this position on the Mt.II, and in *D. sumatrensis* a very large single facet is present.

The proximal region of the right Mt.III (B.U.22031) is preserved, and a distal region (B.U.22032) which is tentatively identified as a Mt.III. The shaft is compressed antero-posteriorly with concave posterior and convex anterior faces. The proximal facet is shallowly concave rising laterally. The bone is transversely narrower than that figured by Fourtau (1920 p. 46 fig. 30) from *B. snowi* and its lateral projection is less pronounced. Paired lateral facets are present for articulation with Mt.IV; these are similar to those of *R. unicornis*. The distal region (B.U.22032) carries a deep transverse channel on the anterior face immediately proximal to the condyle. The facet is relatively small on the anterior face and carries a weak keel on the distal and posterior regions. B.U.22031 and B.U.22032 have no parts in common, and the minimum length of the Mt.III is estimated as 200 mm which agrees closely with that estimated for the Mc.III and is in the right range to accommodate the Mt.IV which is completely known.

Two specimens of the right fourth metatarsal are known (B.U.22037 & B.U.22040). The former is virtually complete lacking only a small part of the posterior distal region, and the latter lacks the proximal and distal posterior regions. The bone is curved laterally (Pl. 5 fig. 6), but less so than the Mt.II; its shaft is long and slender (Pl. 5 fig. 6) and the distal facet is narrow. The proximal facet is very large, swelling sharply from the shaft; it is shallowly convex whereas in *D. sumatrensis* and *R. unicornis* it is shallowly concave. The median facets for articulation with the Mt.III are poorly marked due to erosion of the surface, but they appear to agree with those of *R. unicornis*.

*Phalanges.* A phalange I of a posterior median digit (B.U.22043) is of the long-limbed type and is longer and wider than those from East Africa. A phalange II of a median digit (B.U.22048) may be anterior or posterior, but is also of the long-limbed type.

Four lateral, hind, first phalanges are preserved; they are similar in size and proportions to those of the long-limbed rhinoceroses from East Africa.

## Genus ***BRACHYPOTHERIUM*** Roger 1904

DIAGNOSIS. Large hornless rhinoceroses: $I^1$ and $I_2$ developed as tusks; upper molars with strong antecrochet; crista and crochet usually well developed; protocone strongly constricted; limbs short.

COMMENTS. This group of large, heavy-bodied rhinoceroses is basically defined by the presence of upper tusks ($I^1$) and short limbs and feet. Although the genus was established in 1904, confusion between *Teleoceras* and *Brachypotherium* persisted for the next twenty years, and the name *Teleoceras* was given to the North African brachypothere by Fourtau (1918, 1920). Stehlin (1925), with particular reference to *B. brachypus*, expressed his preference for the use of the name *Brachypotherium* rather than *Teleoceras* as the generic identity had never been demonstrated. After this the generic distinction between the Old and New World forms was usually maintained. The main, easily usable, distinction between the two genera lies in the metapodials, which are more abbreviated in *Teleoceras* than in *Brachypotherium* (Hooijer 1968 and pers. comm.).

### ***Brachypotherium snowi*** (Fourtau) 1918

DIAGNOSIS. A large species of *Brachypotherium* from the Upper Oligocene or Lower Miocene of North Africa. Upper cheek teeth measuring about 300 mm $P^1$–$M^3$. Feet less shortened than in the advanced brachypotheres. Outer faces of lower cheek teeth flattened.

COMMENTS. This species was established under the generic name *Teleoceras* by Fourtau but, as explained above, it was later regarded as a member of the genus *Brachypotherium*. The date of Fourtau's original description seems to be confused ; he gives the date 1918, but Hopwood and Hollyfield (1954) state that this paper ' is a ghost ' and cite all Fourtau's species as being established in 1920 – the date of the publication housed in the British Museum (Natural History). Simons (1969) states that a copy of the 1918 publication is housed in the Osborn Library, American Museum of Natural History. I have treated the 1918 date for the description of the Moghara species as valid.

AGE AND LOCALITY. Lower Miocene ; Moghara, and Siwa, Egypt ; and Gebel Zelten, Libya.

MATERIAL.

M.29382 : a cast of the holotype ; a right maxilla with $P^2$ to $M^3$ all heavily worn (figured Fourtau 1920 p. 38 fig. 26).
M.29384 : a cast of the $P^3$ exhibiting heavy wear (figured Fourtau 1920 p. 39 fig. 2a).
M.29269 : a fragment of right maxilla with $M^1$ and $M^2$ exhibiting medium wear.
M.29268 : a left maxillary fragment with $P^2$ and $P^3$ exhibiting wear.
M.29260 : a fragment of a right mandible with $P_3$–$M_1$.
M.29261 : a fragment of a right mandible with an unerupted $M_3$.
M.29262 : a fragment of a right mandible with $D_2$–$D_4$ in wear and $M_1$ almost fully erupted.
M.29263 : an $I_2$ lacking the tip of the crown and most of the root.
M.29264 : a mandibular symphysis with the $I_1$ and $I_2$ alveoli preserved.
M.29265 : an isolated $I_1$.
M.25126 : the horizontal ramus of a right mandible.
B.U.22025 : a left mandible with $D_1$ to $D_4$ and an unerupted $M_1$.
B.U.22026 : a left vertical ramus of a mandible.

DESCRIPTION.

*Mandible.* M.25126 is an almost complete horizontal ramus which is shallower than that of *R. unicornis* and agrees in depth with M.29260. In M.25126 the cheek teeth are represented by the roots only with the exception of $M_3$, on which a fragment of enamel is preserved ; a two rooted $P_1$ was present on this specimen. The length of the tooth row agrees with that of *B. snowi* from Moghara. The symphysis begins at the level of the middle of $P_2$ and on M.25126 the anterior mental foramen also lies at this level; this foramen is slightly more anteriorly situated in M.29260. The roots of the $I_2$ extend below the $P_2$ in M.25126, M.29260 and M.29264. M.29265 is a complete symphysial region, with both $I_2$ alveloi preserved and the roots of the first incisors (Pl 6 fig. 3). The $I_2$ alveoli run almost parallel to each other, and the teeth would have pointed anteriorly and slightly upwards.

A complete ascending ramus (B.U.22026) is preserved and identified with *Brachypotherium*, mainly on a size basis. The leading edge of the ramus is very broad with a shallow concavity in the region postero-dorsal to $M_3$; this is also present on M.29261 and B.U.22025. M.29261 is larger than would be expected in *Aceratherium*. The medial face of the ramus is concave in the lower part, with a large mandibular foramen which is directed postero-dorsally; the lateral face is plane and the angle is only slightly pronounced. The coronoid process is long antero-posteriorly and low as in *D. schleiermacheri*, and in contrast to *A. incisivum* in which it is short and high. The coronoid of *B. aurelianensis* is similar to that of *B. snowi* in shape and orientation. The condyle is wide and a strong post-condylar process is present as in *B. aurelianensis*, *D. schleiermacheri* and *A. incisivum*. The mandibular fragment found in association with the uncollected skull (Pl. 3) has a length of about 220 mm from the lowest point of the angle to the top of the condyle as measured from the photograph. In B.U.22026 this distance is 280 mm.

*Upper dentition*. The species *B. snowi* was established on the basis of an upper right tooth row in which all the teeth were heavily worn, a more lightly worn, isolated $P^3$, and a very lightly worn $P^4$. Casts of the upper tooth row (M.29382) and the isolated $P^3$ (M.29384) were available for comparisons. Other specimens used are: M.33527 – an upper, left tooth series of *B. brachypus* from Villefranche d'Astrac (Gers), which is made up of teeth from different individuals and was also used by Hooijer (1966 p. 145) in his description of *B. heinzelini*; M.7622 – an isolated left $M^2$ of *B. aurelianensis* from Chilleurs-aux-bois (Loiret), France; M.40743 – an isolated $M^1$ or $M^2$ of *B. goldfussi* from Sansan, Gers, France.

The specimens of *B. snowi* from Gebel Zelten consist of a maxillary fragment with $M^1$ and $M^2$ (M.29269: Pl. 6 fig. 2), and another fragment with $P^2$ and $P^3$ (M.29268: Pl. 6 fig. 1). The molars are badly cracked, but $M^2$ is complete and $M^1$ lacks only the antero-lingual and lingual regions; these teeth are only lightly worn, but the premolars are very heavily worn.

$M^2$ has a strong protocone constriction with anterior and posterior grooves, and a shallow hypocone groove is also present. Constriction and grooves of similar strength are present in *B. brachypus* and *B. goldfussi*, but they are stronger in *B. aurelianensis*. The strength of these features is to some extent related to the strength of the antecrochet; this is strong in M.29269 and in *B. snowi* from Moghara; it is similar in strength in *B. brachypus* and *B. goldfussi*, but is stronger in *B. aurelianensis*. A weak fold of the enamel near the labial end of the medisinus suggests the presence of a crista, and a strong crochet is present; a crochet of similar strength is present in *B. brachypus* but in *B. goldfussi* and *B. aurelianensis* the crochet is stronger. A crista is not present in specimens of *B. brachypus* figured by Deperet (1887 pl. 23 figs. 1 & 1a) and Mayet (1909 p. 25 fig. 11), nor in *B. aurelianensis* figured in Mayet (1908 pl. 2 fig. 5); this suggests that the crista is variable in the brachypotheres. The metaloph is flexed posteriorly in M.29269 (Pl. 6 fig. 2) as in *B. brachypus* and *B. aurelianensis* ; this flexion is stronger than in the Gebel Zelten acerathere and produces a deep postfossette. The parastyle and paracone ribs are very strong and similar to those of *B. snowi* from Moghara, with a weaker labial extension than in *B. brachypus*, *B. aurelianensis* or *B. goldfussi*. The labial face of the ectoloph is concave with a swelling opposite the mesostyle. The anterior and posterior cingula are strong as in M.29382 from Moghara. A small swelling of enamel at the base of the postero-labial corner may represent a labial cingulum, but otherwise labial and lingual cingula are absent except at the entrance to the medisinus ; this contrasts with *B. brachypus* and *B. goldfussi* in which strong lingual and labial cingula are present. However, variation in the strength or presence of the cingula occurs (Viret 1961).

An isolated $M^3$ from Siwa, Libyan Desert, Egypt, was identified with *B. snowi* (Hamilton 1973). It is smaller than the $M^3$ of the type dentition (Fourtau 1920 p. 38 fig. 26), and lacks the antero-lingual rib which is produced from the face of the hypocone ; it also differs in several features from the $M^3$ of *B. heinzelini* (M.10632).

The $P^3$ (M.29268) agrees closely with that described by Fourtau (1920 p. 39 fig. 3a) ; it is very heavily worn (Pl. 6 fig. 1) and details of the crown are largely worn away. The $P^2$ (M.29268) is also similar to that of *B. snowi* from Moghara (M.29382).

The upper dentition of *B. snowi* compares closely in general features with that of *B. brachypus*, but the parastyle and paracone region is less pronounced antero-lingually, and the lingual cingula are either weak or totally absent. There are also differences in the strengths of the antecrochet, crochet and crista, but these features exhibit variation in *B. brachypus*, and their significance here cannot be assessed as so few specimens of *B. snowi* are known.

*B. heinzelini* from East Africa and the Congo is represented in the British Museum (Natural History) collections by an isolated $M^3$ (M.10632), which was figured as an unidentified rhinocerotid by Andrews (1914 pp. 176–177 pl. 28 fig. 3), and was identified with *B. heinzelini* by Hooijer (1966 pl. 7 fig. 3). Good dental material of this species appears to be relatively scarce, as Hooijer (1963, 1966) figures very little material. The holotype is a $P^4$ from Sinda, Congo, which was briefly compared with *B. snowi* by Hooijer (1963 p. 46). The tooth appears to be very similar in the two species, but a labial cingulum is present in *B. heinzelini* from the Congo, though absent in the Rusinga specimen (Hooijer 1966 p. 143) and in the $P^4$ of *B. snowi*. The $P^4$ is generally longer and narrower in *B. heinzelini* than in *B. snowi*. The $M^1$ of *B. heinzelini* from Karungu (Hooijer 1966 pl. 6 figs. 5 & 6) is very heavily worn and appears very different in shape in comparison with that of *B. snowi*. This specimen has a labial cingulum which contrasts with the molars of *B. snowi* in which the labial cingulum is very reduced if present. An $M^2$ of *B. heinzelini* is also figured by Hooijer (1963 pl. 8 figs. 4–6) under the name *Aceratherium cf. tetradactylum* ; reasons for the reidentification of this specimen are given by Hooijer (1966 p. 143). This $M^2$ compares in general features with the Zelten specimen (Pl. 6 fig. 2), but the labial wall is more flattened, the antecrochet is stronger and the crochet appears double in the Congo specimen. The tooth also differs in size from that of *B. snowi*.

On the basis of these comparisons I think that the upper dentition of *B. snowi* is distinct from that of *B. heinzelini*.

The incidence of *Indricotherium* (*Paraceratherium*) at Sahabi, Libya, was noted by Savage (1967) and Hooijer (1968), the record being based upon an isolated rhinocerotid $M^2$ described as *Teleoceras aff. medicornutum* by Erasmo (1954), and identified with *Indricotherium* by Hooijer (1968) on account of its great size. This tooth is very similar to the $M^2$ of *B. snowi*, having a strong protocone constriction with a marked posterior protocone groove. A strong antecrochet and crista and a weak swelling suggests that a small crochet may have been present. The tooth is, however, much larger than the $M^2$ of *B. snowi*, having an anterior width of 99 mm, a posterior width of 92 mm and a length of 78 mm. The Sahabi fossils are of late Miocene age, and during the interval between the time of deposition of the Gebel Zelten and Sahabi an increase in size of a *Brachypotherium* stock could well have occurred. In my opinion the Sahabi specimen represents a survival of *Brachypotherium* into the late Miocene of Libya.

*Lower dentition* : *incisors*. A single left $I_2$ is preserved (M.29263 : Pl. 6 fig. 8) ; this agrees closely with the $I_2$ of *B. brachypus* figured by Roman & Viret (1934 pl. 11 fig. 5), and with that of *B. aurelianensis* figured by Mayet (1908 pl. 3 fig. 2), and is almost exactly the same size as these incisors. The root is elliptical in cross-section with the long diameter horizontal. This contrasts with *D. leakyi* in which the root of the incisor has a subtriangular cross-section (Hooijer 1966). The root of M.29263 is straight antero-posteriorly and curves slightly dorsally as in *B. aurelianensis* (Mayet 1908 pl. 2 fig. 2a), and in agreement with the curvature of the alveoli in M.25126 and M.29264, which also have similar cross-sections. The crown of the tooth is heavily worn but it flares laterally immediately above the root as in *B. brachypus*, *B. aurelianensis* and *Chilotheridium* (Hooijer 1971 pl. 6 figs. 1–4) ; this sort of expansion is not visible in *D. leakyi* (Hooijer 1966 pl. 4 figs. 4 & 5), *D. schleiermacheri* (M.21490), *A. incisivum* (M.253) or *A. acutirostratum* (Hooijer 1966 pl. 4 figs. 2 & 3). The tip of the crown is broken off (Pl. 6 fig. 8), but it was lance shaped with the point on the medial side. Preserved parts of the tooth agree closely with the $I_2$ of *B. brachypus* in which the root length is 110 mm suggesting a similar root length for M.29263 ; this agrees with the length of the alveoli in M.29264. The crown of the tooth is heavily worn with facets in two planes (Pl. 6 fig. 8). The medial facet is the more horizontal and its surface is smooth : it blends laterally into a more laterally directed facet, which has deep transverse striations indicating heavy wear against a hard object – presumably the $I^1$.

An isolated $I_1$ (M.29265 : Pl. 5 fig. 3) is preserved with fragments of the alveoli ; the tooth is tentatively identified with *B. snowi* as its root has the same cross-sectional shape as the $I_1$ roots in the symphysis (M.29264), though the isolated tooth is larger. The root curves dorsally and the $I_1$ would have projected anteriorly at approximately the same angle as the $I_2$. The crown is bulbous and exhibits heavy wear on its tip ; similar first lower incisors are present in *R. unicornis*.

*Cheek dentition*. The lower cheek teeth identified with *Brachypotherium* are larger and higher than those of *Aceratherium*. In agreement with Hooijer (1966) the depth of the groove between the hypolophid and metalophid was taken as a

TABLE 8

Upper dentition of *Brachypotherium snowi*

| | *B. snowi*, Gebel Zelten | | *B. snowi*, Moghara | | *B. snowi*, Siwa | *B. heinzelini* | | *B. brachypus* |
|---|---|---|---|---|---|---|---|---|
| | M.29269 | M.29268 | M.29382 | M.29384 | M.11966 | Congo | E. Africa | M.M.33527 |
| $P^2$ | | | | | | | | |
| Antero-posterior length | – | 32 | 29 | – | – | – | – | 30 |
| Anterior transverse width | – | 39 | 42 | – | – | – | – | 39 |
| Posterior transverse width | – | 42 | 45 | – | – | – | – | 43 |
| $P^3$ | | | | | | | | |
| Antero-posterior length | – | 41 | 40 | 40 | – | – | 36 | 34 |
| Anterior transverse width | – | 60 | 61 | 60 | – | – | 54 | 51 |
| Posterior transverse width | – | 54 | 56 | 56 | – | – | 54 | 52 |
| $P^4$ | | | | | | | | |
| Antero-posterior length | – | – | 44 | – | – | 49 | 48 | 39 |
| Anterior transverse width | – | – | 70 | – | – | 62 | 66 | 58 |
| Posterior transverse width | – | – | 61 | – | – | 58 | 62 | 55 |
| $M^1$ | | | | | | | | |
| Antero-posterior length | 56 | – | *c* 53 | – | – | – | – | 54 |
| Anterior transverse width | – | – | 71 | – | – | – | 62 | 70 |
| Posterior transverse width | – | – | 62 | – | – | – | 52 | 60 |
| $M^2$ | | | | | | | | |
| Antero-posterior length | 62 | – | 61 | – | – | 63 | – | 52 |
| Anterior transverse width | 79 | – | 75 | – | – | 77 | – | 68 |
| Posterior transverse width | 67 | – | 63 | – | – | 63 | – | 58 |
| $M^3$ | | | | | | | | |
| Antero-posterior length | – | – | 61 | – | 54 | – | 55 | 56 |
| Anterior transverse width | – | – | – | – | – | – | 65 | 68 |
| Length of outer face | – | – | – | – | – | – | 68 | 73 |

criterion on which the lower cheek teeth of *Aceratherium/Dicerorhinus* and *Brachypotherium* could be distinguished; those teeth with shallow grooves were placed with *Brachypotherium* and those with deep grooves were identified with *A. campbelli.* This distinction is, however, not invariable, teeth with shallow grooves usually belong with *Brachypotherium* but those with deep grooves may belong with either *Dicerorhinus/Aceratherium* or with *Brachypotherium.* This is demonstrated by the mandible identified with *B. snowi* by Fourtau (1920); cheek teeth on this mandible have deeper grooves than on the lower molars identified with *B. snowi* from Gebel Zelten, but its identification with *B. snowi* is probably valid (Hooijer pers. comm.). A cast of Fourtau's specimen (M.29383), lower cheek teeth of *B. brachypus* (M.33523), lower molars of *B. goldfussi* (M.238 : Kaup 1834 pl. 12 figs. 13 & 14) and a lower molar fragment of *B. heinzelini* (M.25186) were available for comparison.

The $M_1$ of *B. snowi* has weak anterior and posterior cingula and two small tubercles at the lingual opening of the posterior valley (Pl. 6 fig. 4). The hypolophid is much longer than the metalophid, a feature also exhibited by *B. brachypus* and *B. goldfussi*, and the labial groove is weaker than in these species, though similar in strength to that of *B. heinzelini* (M.25186).

M.29261, an unerupted lower molar, is probably an $M_3$; its labial groove is slightly stronger than in M.29260 but far weaker than in *Aceratherium.* The molar is relatively high and the hypolophid–metalophid junction is over 30 mm above the base of the crown. A weak posterior cingulum is present.

The $P_4$ is more elongate than in *B. brachypus* and appears less antero-posteriorly compressed, as the lingual valleys are more open and the anterior end of the metalophid is less flexed lingually (Pl. 6 fig. 4). The hypolophid also exhibits less flexion, cingula are absent and the labial groove is very shallow (Pl. 6 fig. 6). The $P_4$ of *B. snowi* from Moghara has a deeper labial groove than that of M.29260 and although heavily worn it appears that the crown was lower. The posterior lingual valley was deeper and its opening extends more nearly to the base of the crown. The $P_3$ of M.29260 differs from *B. brachypus* in the same features as the $P_4$, it is more elongate and less antero-posteriorly compressed, the lingual valleys are more open and the anterior end of the metalophid is less flexed lingually. A weak cingulum is present on the antero-labial corner only, whereas in *B. brachypus* cingula are present on the four corners though in M.33523 they do not join across the faces of the tooth. The groove at the junction of the metalophid and hypolophid is relatively strong on the $P_3$ of *B. brachypus* and on *B. snowi* from Moghara but in M.29260 it is very shallow. The $P_3$ of *B. snowi* from Moghara resembles the $P_4$ in having a heavily worn and probably initially lower crown with a deeper posterior lingual valley. A $P_2$ of *B. snowi* is not known from Gebel Zelten but Fourtau (1920) describes a $P_2$ and a fragment of the $P_1$ of *B. snowi* from Moghara. A $P_1$ was probably not present in M.29260 but the presence of a $D_1$ in B.U.22025 suggests that the presence of a $P_1$ may have been variable.

Descriptions of the deciduous lower dentitions of rhinoceroses are rare in the literature. Roman & Viret (1934 pl. 10 fig. 9) describe and figure a lower deciduous cheek tooth of *B. brachypus* which is probably a $D_3$ and Hooijer (1966 pl. 4 fig. 1) figures the $D_2$–$D_4$ of *Dicerorhinus leakyi* from Napak, Uganda. M.29262 is a crushed

TABLE 9

Lower dentition of *Brachypotherium snowi*

| INCISOR | M.29263 |
|---|---|
| Width of crown | 40 |
| Antero-posterior length of crown | 26 |
| Transverse diameter of crown | 36 |
| Antero-posterior diameter of root | – |

| CHEEK TEETH | M.29260 | M.29261 | M.29262 | Moghara | *B. heinzelini* E. Africa | *B. brachypus* M.33523 |
|---|---|---|---|---|---|---|
| $P_2$ | | | | | | |
| Antero-posterior length | *c* 22 | – | – | 28 | – | – |
| Anterior transverse width | – | – | – | 18 | – | – |
| Posterior transverse width | – | – | – | 22 | – | – |
| $P_3$ | | | | | | |
| Antero-posterior length | 34 | – | – | 36 | – | 39 |
| Anterior transverse width | 20 | – | – | 25 | – | 24 |
| Posterior transverse width | 24 | – | – | 26 | – | 28 |
| $P_4$ | | | | | | |
| Antero-posterior length | 42 | – | – | – | – | 49 |
| Anterior transverse width | 20 | – | – | – | – | 28 |
| Posterior transverse width | 28 | – | – | 28 | – | 32 |
| $M_1$ | | | | | | |
| Antero-posterior length | 46 | – | 51 | – | – | 46 |
| Anterior transverse width | 27 | – | – | – | – | 31 |
| Posterior transverse width | 30 | – | – | – | 29 | – |
| $M_2$ | | | | | | |
| Antero-posterior length | – | – | – | 57 | 56 | 54 |
| Anterior transverse width | – | – | – | – | 37 | 33 |
| Posterior transverse width | – | – | – | 37 | 35 | 33 |
| $M_3$ | | | | | | |
| Antero-posterior length | – | 53 | – | *c* 62 | – | 61 |
| Anterior transverse width | – | 31 | – | | 31 | 33 |
| Posterior transverse width | – | *c* 30 | – | *c* 34 | 29 | 33 |

fragment of a right mandible containing the almost complete $D_2$–$D_4$ and the labial and anterior regions of the partially erupted $M_1$ (Pl. 7 figs. 3 & 4). This specimen is identified with *B. snowi* as the $M_1$ agree with other lower molars of this species. B.U.22025 is also identified with *Brachypotherium*; it contains $D_1$–$D_4$ and an unerupted $M_1$ (Pl. 8). The $D_1$ is small, single rooted and peg-like. $D_2$ is triangular and trilobed with two labial and two lingual grooves. $D_3$ is elongate and molariform; it exhibits medium wear in B.U.22025 and heavier wear in M.29262. The anterior end of the anterior lophid is forked as in the $D_3$ of *B. brachypus* (Roman & Viret 1934 pl. 10 fig. 9). The $D_3$ lacks a labial cingulum. Hooijer (1971) discusses a $D_3$ from Ngorora which he identifies with *Brachypotherium*. This tooth has a weak labial cingulum and a $D_3$ of *Brachypotherium* from Lothagam also has a weak cingulum. Both of these teeth are in the same size range as M.29262 and B.U.22025.

The $D_4$ is molariform with well-developed lophids and a weakly developed labial groove; it is about the same length as the $D_3$ and carries a cingulum in its antero-lingual region. The fragment of the $M_1$ in M.29262 is hypsodont and the metalophid is shorter than the hypolophid as in M.29260; the labial groove is also shallow in M.29262. The unerupted $M_1$ of B.U.22025 has a slightly stronger labial groove but is larger and more hypsodont than the $M_1$ of the Zelten *Aceratherium*. Fourtau also described an isolated $M_2$ which had a flattened outer face and carried a cingulum anteriorly. This agrees with *B. brachypus* and a weak swelling on the face of the tooth in this region is also present on the $M_1$ of M.29260. The $M_2$ described by Fourtau is relatively large, having a length of 57 mm. This isolated molar agrees in size with M.29260 and M.29262 and probably belongs with the same species. Fourtau also gives the dimensions of the alveoli of the $M_3$ from the same mandible as the $M_2$; this tooth had alveoli of length 62 mm and width 34 mm (Table 9), which is larger than M.29261 but within the same size range and far outside the size range of M.29254 which is here identified with *Aceratherium*.

### Table 10

Lower deciduous dentition of *Brachypotherium snowi*

| | M.29262 | B.U.22025 |
|---|---|---|
| $D_1$ | | |
| Antero-posterior length | – | 8 |
| Transverse width | – | 5 |
| $D_2$ | | |
| Antero-posterior length | 31 | 29 |
| Anterior transverse width | 15 | 13 |
| Posterior transverse width | 20 | 17 |
| $D_3$ | | |
| Antero-posterior length | 47 | 42 |
| Anterior transverse width | 24 | 18 |
| Posterior transverse width | 25 | 21 |
| $D_4$ | | |
| Antero-posterior length | 49 | 45 |
| Anterior transverse width | 27 | 21 |
| Posterior transverse width | 30 | 25 |

*Post-cranial material.* Dental evidence suggests that only a single short-limbed rhinoceros was present at Gebel Zelten in early Miocene times, and post-cranial elements characteristic of short-limbed rhinoceroses may therefore be assigned to the genus *Brachypotherium*. It is likely that *Brachypotherium* was the only short-limbed rhinoceros in Africa in early Miocene times, as records of *Chilotherium* from Africa south of the Sahara are no longer valid, and *Chilotheridium* is a longer-limbed form.

MATERIAL.

M.29274 : a complete right radius.
M.29275 : a complete left, third metacarpal.
B.U.22027 : a badly shattered third metacarpal.
B.U.22028 : a cracked but nearly complete, right, second metacarpal.
B.U.22029 : a complete, right, fourth metacarpal.
M.29278 : a left astragalus.
B.U.22030 : a left astragalus.
M.29279 : a left astragalus.
B.U.22031 : the proximal region of a first phalange of the right, anterior, median digit.
B.U.22032 : the second phalange of a median digit.
B.U.22033 : the second phalange of a median digit.
M.29277 : a left astragalus from Arongo Uyoma, East Africa.

DESCRIPTION.

*Radius.* A complete right radius (M.29274) agrees closely with that of *B. heinzelini* (M.18908) described by Hooijer (1966 pl. 9 fig. 1). The Gebel Zelten specimen is slightly more slender (Table 11), and the distal end is less massive than in *B. heinzelini*. This is the only rhinocerotid radius from Gebel Zelten ; it is shorter and thicker than those of the East African long-limbed rhinoceroses, and is smaller than the radii of *B. brachypus* and *B. stehlini*. In his 1971 paper Hooijer mentions the presence of a small facet on the radius of *Chilotheridium* which articulates with the cuneiform ; such a facet is not present on M.29274 or M.18908.

TABLE 11

*Brachypotherium* Post-cranial material

Radius

| | M.29274 | *B. heinzelini* | *Chilotheridium* |
|---|---|---|---|
| Median length | 282 | 293 | 315 |
| Proximal width | 86 | 95 | 94 |
| Middle width (maximum) | 49 | 52 | 50 |
| Distal width (maximum) | 84 | 95 | 95 |

*Metacarpals.* Metacarpals of *B. heinzelini* from East Africa were available for comparison ; these included Mc.III and Mc.IV (M.18813 & M.18812 : Hooijer 1966 pl. 10 figs. 1 & 2), and Mc.IV (M.18822 : Hooijer 1966 pl. 10 fig. 8).

The Mc.II from Gebel Zelten is large and relatively thick ; the proximal medial facet is concave, rising laterally with a new facet starting at the top of this rise and sloping disto-laterally. The anterior face of the metacarpal is heavily sculptured, and the posterior face carries several tubercular swellings of the bone. This metacarpal agrees in general shape with that figured by Hooijer (1966 pl. 10 fig. 3), but the distal facet is longer on the anterior face and the medio-proximal swelling of the bone is weaker in the Gebel Zelten specimen than in that from East Africa.

The third metacarpals (M.29275 & B.U.22027) agree closely with the Mc.III of *B. heinzelini.* M.29275 (Pl. 6 figs. 5 & 9) is slightly longer than the East African specimen (Table 12), but it is also more massive with a very strong anterior tuberosity in the proximal region and proximal facets for Mc.IV which are larger and more widely separated than in *B. heinzelini.* The distal facet of M.29275 is narrower than in *B. heinzelini* and extends further proximally on the anterior face of the bone ; this facet is also deeper antero-posteriorly in the Gebel Zelten specimen.

The Mc.IV (B.U.22029) is smaller and rather more slender than the East African specimens (M.18812 & M.18813) ; its proximo-medial region is only slightly swollen whereas in the East African Mc.IV this region carries a strong swelling. B.U.22029 is slightly bent laterally but to a smaller extent than in the East African specimens and its distal facet is smaller.

These three metacarpals are difficult to interpret as the Mc.II is large relative to the Mc.III, and similarly the Mc.IV is relatively small ; this is interpreted as falling within the degree of variation of a single species as the alternative interpretation – that there were three short-limbed forms at Gebel Zelten – is unlikely. The Mc.III agrees closely with that of *B. heinzelini*, but is from a slightly larger animal which agrees with differences in the size of the dentition. This metacarpal also agrees closely in size with the Mt.III described from Moghara (Fourtau 1920 p. 46 & text fig. 30), which was identified as *B. snowi.* Metatarsals identifiable with the short-limbed rhinoceroses are not known from Gebel Zelten or East Africa, but Hooijer (1966) compared the Mc.III of *B. heinzelini* with the Mt.III of *B. snowi* by comparing both with *B. brachypus* in which, as Hooijer (1966 table 16) demonstrates, there is considerable variation in the size of the metacarpals and the metatarsals. By this somewhat roundabout method Hooijer deduced that : ' the Rusinga *B. heinzelini* is more progressive than that of Moghara in Egypt in having more shortened metapodials '. The direct comparison of the Mc.III from Gebel Zelten with that from East Africa demonstrates that the metapodials have approximately the same proportions.

*Astragalus.* The astragali of *Brachypotherium* are very compressed and the median height never exceeds the width, whereas in the long-limbed rhinoceroses the median height of the astragalus may be equal to or greater than the width. Astragali of *B. brachypus* (M.33529) from Villefranch d'Astrac and (M.7760) from Thenay were available for comparison ; both were also used by Hooijer (1966). Astragali of *B. heinzelini* are figured by Hooijer (1963 pl. V fig. 10 & 1966 pl. 14 fig. 3). The Zelten astragali are all from the left side. B.U.22030 and M.29278 agree in size with the African and European specimens, but M.29279 (Pl. 6 fig. 7) is larger though similar in proportions and details of the facets.

TABLE 12

*Brachypotherium* Post-cranial material

Metacarpals

| | Mc. II | | | Mc. III | | | |
|---|---|---|---|---|---|---|---|
| | B.U.22028 | *B. heinzelini* | *Chilotheridium* | M.29275 | B.U.22027 | *B. heinzelini* | *Chilotheridium* |
| Length | 149 | 125 | 123 | 146 | 140 | 137 | 140 |
| Proximal width | 51 | 52 | 41 | 75 | – | 65 | 49 |
| Proximal antero-posterior depth | 50 | 47 | 36 | 61 | – | 52 | 38 |
| Middle width | 53 | 45 | 33 | 60 | – | *c* 55 | 39 |
| Middle antero-posterior depth | 31 | 25 | 17 | 25 | – | 26 | 17 |
| Distal width | 57 | 50 | 43 | 74 | – | 74 | 52 |
| Distal antero-posterior depth | 51 | 38 | 37 | 55 | – | 47 | 39 |
| Width of distal trochlea | 48 | 40 | 37 | 58 | – | 58 | 45 |

| | Mc. IV | | |
|---|---|---|---|
| | B.U.22029 | *B. heinzelini* | *Chilotheridium* |
| Length | 103 | 110 | 115 |
| Proximal width | 31 | 44 | 37 |
| Proximal antero-posterior depth | 35 | 53 | 44 |
| Middle width | 31 | 37 | 26 |
| Middle antero-posterior depth | 20 | 25 | 18 |
| Distal width | 41 | 53 | 41 |
| Distal antero-posterior depth | – | 38 | 33 |
| Width of distal trochlea | 32 | 45 | 36 |

TABLE 13

*Brachypotherium* Post-cranial material

Astragalus

| | Gebel Zelten | | | *B. brachypus* | | Arongo Uyoma | *B. heinzelini* |
|---|---|---|---|---|---|---|---|
| | M.29278 | B.U.22030 | M.29279 | M.33529 | M.7760 | M.29277 | Congo[1] |
| Lateral height | 69 | 68 | 73 | 58 | 60 | 58 | 68 |
| Medial height | 67 | 68 | 75 | 64 | 63 | 55 | – |
| Total width | 105 | 93 | 113 | 100 | 99 | 87 | 102 |
| Ratio medial height/total width | | | | | | | |
| Trochlea width | 75 | 75 | 90 | 85 | 80 | 75 | – |
| Width of distal facets | 91 | 84 | 95 | 85 | 86 | 68 | – |

([1] after Hooijer 1963)

An isolated astragalus from Arongo Uyoma, East Africa (M.29277), was missed by Hooijer (1966). Its details are given here, as the astragali of short-limbed rhinoceroses are relatively rare from East Africa and this is the only such astragalus in the British Museum (Natural History) collection. The bone is from the left side, and the lateral half is complete except on the antero-lateral face of the left trochlear ridge from which a chip of bone is missing. The medial distal part is well preserved but the medial proximal region is broken off. This astragalus is similar in size and general features to the Gebel Zelten specimens (M.29278 & B.U.22030), and also agrees with the astragali of *B. heinzelini*. The disto-lateral facet is correspondingly smaller ; this is, however, only a slight variation, and I think this specimen is probably from *B. heinzelini*.

*Phalanges*. The proximal region of the first phalange of the right, anterior, median digit (B.U.22031) carries a strong swelling of the bone which forms a collar around the bone just distal to the articulation. A similar swelling is present on the phalange I of *B. heinzelini* (Hooijer 1966 pl. 10 fig. 6), which suggests that this bone may belong with the short-limbed rhinoceroses. The posterior face of the bone falls away anteriorly indicating that it was much compressed. The proximal facet of the phalange is narrower than that of *B. heinzelini* and also narrower than the distal facet of Mc.III (M.29275) identified with *B. snowi*.

Two second phalanges of median digits – B.U.22032 and B.U.22033 – are more proximo-distally compressed than in the long-limbed rhinoceroses and probably belong with the short-limbed group. However, each is longer than the phalange II of *B. heinzelini* (M.18862 : Hooijer 1966 pl. 10 fig. 7).

A few carpals and tarsals are probably identifiable with *B. snowi*, but these are described with the other elements from Gebel Zelten as identification is less certain and direct comparison is simplified.

## Rhinocerotidae indet.

The following specimens cannot be definitely assigned to either groups of rhinoceroses known from Gebel Zelten.

M.29305 : an isolated right scaphoid.
B.U.22051 : fragment of a lunar.
B.U.22050 : fragment of a lunar.
M.29306 : cuneiform.
M.29307 : cuneiform.
B.U.22052 : cuneiform.
B.U.22053 : left trapezoid.
M.29293 : calcaneum.
B.U.22054 : right calcaneum.
B.U.22055 : right calcaneum.
B.U.22056 : right calcaneum.
B.U.22057 : left calcaneum.
B.U.22058 : right calcaneum.
M.10364 : calcaneum from East Africa.

M.29308 : right cuboid.
B.U.22059 : left cuboid.
B.U.22060 : right cuboid.
B.U.22062 : left navicular.
M.29310 : right navicular.
B.U.22061 : right navicular.
B.U.22064, B.U.22063, B.U.22065, B.U.22066, M.29312 : ectocuneiforms.

*Scaphoid*. An isolated right scaphoid M.29305 is large and agrees closely in size with M.18897 from East Africa (Hooijer 1966 table 30 & pl. 14 fig. 6), and with that of *D. schleiermacheri* (M.1218 : Kaup 1834 pl. 13 fig. 9). The distal articular facet of the radius and corresponding facet of the scaphoid agree, suggesting that the scaphoid belongs with the short limbed rhinoceroses, but this may be a size factor.

Table 14

Rhinocerotidae indet. Post-cranial material

Scaphoid

| | M.29305 | E. Africa M.18897 |
|---|---|---|
| Posterior height | 68 | 71 |
| Anterior height | 60 | 54 |
| Proximal width | 49 | 49 |
| Distal width | 34 | 33 |
| Antero-posterior middle length | 68 | 66 |

*Lunar*. Two fragmentary lunars are known. B.U.22051 lacks the proximal radius facet and the posterior region of the bone is broken off. B.U.22050 consists of the anterior region only ; the anterior proximal facet for articulation with the radius is preserved and the distal unciform facet. The radius facet is antero-posteriorly convex and similar to that of M.18907 from East Africa (Hooijer 1966 p. 163) ; this facet is transversely narrower than in *R. unicornis* (M.O.1961.6.10.1). B.U.22051 is deeper proximo-distally than in *R. unicornis*, agreeing with M.18907 from East Africa. The distal facets for the magnum and unciform are less concave than in M.18907 ; the unciform facet agrees closely with that of *R. unicornis* but the magnum facet is smaller and shallower.

Table 15

Rhinocerotidae indet. Post-cranial material

Lunar

| | B.U.22051 | B.U.22050 | E. Africa M.18906 | E. Africa M.18907 |
|---|---|---|---|---|
| Anterior height | – | 55 | 45 | 48 |
| Proximal width | – | 44 | 45 | – |
| Greatest antero-posterior length | *c* 68 | – | – | 67 |

*Cuneiform.* The three cuneiforms are all complete and all are larger than those from East Africa (Table 16). M.29306 is more compressed proximo-distally than the other two, and is very wide transversely and long antero-posteriorly. The proximal facet for the ulna is antero-posteriorly concave and transversely convex giving a saddle-shaped form ; this facet remains wide laterally whereas in M.29307 and B.U.22052 it tapers to a point laterally ; this also occurs in *R. unicornis* and *D. schleiermacheri* and the three specimens from East Africa (M.18903, M.25184 & M.18904). The facet for the pisiform is large and triangular. The distal facet for articulation with the unciform is more shallowly concave than in M.29307 or B.U.22052. M.29306 carries a large tubercle disto-laterally ; this swelling is far larger than any of the East African specimens, *R. unicornis, D. sumatrensis*, M.29307 or B.U.22052. Features of M.29306 suggest very strongly that it belongs with the short-limbed rhinoceroses, and it agrees closely with a cuneiform from Gers, France (M.33537), which probably belongs to *B. brachypus.*

M.29307 and B.U.22052 are long proximo-distally, the former less so than the latter (Table 16). In features of the facets these specimens agree closely with the cuneiform of *R. unicornis* and contrast with M.29306 as described above. These two specimens probably belong with the long-limbed rhinoceroses.

*Trapezoid.* An isolated left trapezoid is longer proximo-distally than that of *R. unicornis* and as a result its proximal and distal facets do not meet. The bone is broken antero-laterally.

*Calcaneum.* The nomenclature applied here to the calcaneum is after Schaeffer (1947). Calcanea from Gebel Zelten exhibit variation in size and features of the facets. The tuber calcis varies in length and the shaft is very thick in M.29293 and B.U.22054 but is transversely flattened in the other four specimens. The astragalocalcaneal facet is strongly convex proximo-distally in M.29293 and B.U.22054 as in *D. schleiermacheri* (M.2785 : Kaup 1834 pl. 13 fig. 10) and *A. incisivum* (M.1288 : pl. 15 fig. 11), but in the other four specimens this facet rises steeply from its distal region and curves very sharply. It then flattens out and continues for some distance along the proximal face of the tuber, thus giving two regions – a vertical and a horizontal – of approximately equal size, at right angles to each other.

The sustentaculum is strong and wide in M.29293, with a wide, almost circular sustentacular facet which is shallowly concave. This region is also preserved in B.U.22025, in which it is less pronounced and carries a narrow, proximo-distally elongate, sustentacular facet. A fragment of this region is preserved on B.U.22056 and indicates a similarly shaped facet.

The astragalar facet is similar in all the specimens. The cuboid facet is antero-posteriorly concave and almost circular in M.29293 and B.U.22054, but in the other four specimens it is narrow and deeply concave transversely. The peroneal tubercle is variable in strength, being very strong in M.29293 and B.U.22054, slightly weaker in B.U.22055 and B.U.22056 and very weak in B.U.22057 and B.U.22058. A second tubercle on the lateral face lying behind and slightly proximal to the peroneal tubercle is very strong in M.29293 and B.U.22054, but is weak in the other four specimens.

TABLE 16

Rhinocerotidae indet. Post-cranial material

Cuneiform

| | | | | | E. Africa | | *B. brachypus* ? |
|---|---|---|---|---|---|---|---|
| | M.29306 | M.29307 | B.U.22052 | M.25184 | M.18903 | M.18994 | M.33637 |
| Anterior height | 60 | 58 | 63 | 50 | 38 | – | 48 |
| Distal width | 73 | 55 | 51 | 36 | 32 | 33 | 50 |
| Proximal antero-posterior length | 44 | 38 | 37 | 27 | 26 | 32 | 40 |
| Greatest horizontal diameter | 74 | 58 | 56 | 40 | – | 42 | 50 |

TABLE 17

Rhinocerotidae indet. Post-cranial material

Trapezoid

| | B.U.22053 | *Chilotheridium*[1] |
|---|---|---|
| Anterior height | *c* 35 | 30 |
| Anterior width | 26 | 24 |
| Greatest antero-posterior diameter | 45 | 41 |
| Posterior height | 37 | 28 |
| Posterior width | 31 | 16 |

[1] After Hooijer 1971.

From the above comparison it is clear that the calcanea may be divided into two groups, one including M.29293 and B.U.22054 and the other containing the four specimens B.U.22055 to B.U.22058. The calcanea in the first group agree closely with that of *D. schleiermacheri*, and possibly belong with the long-limbed rhinoceroses.

An isolated calcaneum from East Africa (M.10364) was missed by Hooijer (1966) in his review of the East African material. As rhinocerotid calcanea are so rare in the East African collections a brief description of this specimen is given here. The shaft of the tuber calcis is transversely thickened and the distal end of the tuber is wide and heavily sculptured. The astragalocalcaneal facet is convex and similar to that of M.29293, but this region of the bone rises well above the face of the tuber calcis in M.10364, whereas in the Zelten specimens and *D. schleiermacheri* it is much lower. The sustentaculum is missing and the astragalar facet is reduced. The cuboid facet is antero-posteriorly concave and almost circular, agreeing with that of M.29293. This specimen agrees closely in general form and features with that of *D. schleiermacheri*, and in size with that of *D. leakyi* (Hooijer 1966 table 44). It may therefore be placed with the East African long-limbed rhinoceroses.

*Cuboid.* M.29308 is almost complete, its proximal facet is antero-posteriorly concave and transversely convex. The lateral region of the facet, for articulation with the calcaneum, is larger than the medial region of the facet and is separated from this region by a shallow antero-posterior channel. The distal facet for articulation with the Mt.IV is antero-posteriorly elongate and convex in M.29308, but in B.U.22059 it is transversely wide and convex agreeing with the facet of M.18890 from East Africa. The posterior projection of the bone is very strong in M.29308, B.U.22059, and in M.18892 from East Africa. The medial facets for articulation with the navicular and ectocuneiform are very small in M.29308 as in *R. unicornis* (M.O.1961.5.10.1), in which they are smaller than in M.18892 from East Africa. These facets are broken off B.U.22060. M.29308 is long proximo-distally and is transversely narrower than B.U.22059, B.U.22060, M.18892 or M.18890, but the antero-posterior length is similar in B.U.22059 and M.29308 (Table 19). B.U.22060 is a fragment of a high cuboid which agrees in size and proportions of its facets with B.U.22059. According to Roger (1900 p. 24), the anterior face of the cuboid is much wider than high in *Brachypotherium* : in *Aceratherium* and *Dicerorhinus* the anterior height of the cuboid is equal to or greater than the anterior width. This

TABLE 18

Rhinocerotidae indet. Post-cranial material

Calcaneum

| | Gebel Zelten | | | | | | E. Africa | |
|---|---|---|---|---|---|---|---|---|
| | M.29293 | B.U.22054 | B.U.22055 | B.U.22056 | B.U.22057 | B.U.22058 | M.10364 | *D. leakyi* |
| Greatest length | 131 | 140 | 119 | 143 | 143 | 149 | 136 | 148 |
| Greatest width | 82 | – | 64 | – | – | – | – | 89 |
| Antero-posterior cuboid facet | 36 | 40 | 40 | 47 | 45 | 49 | 46 | 48 |
| Transverse cuboid facet | 29 | – | 22 | 25 | 26 | 23 | 34 | 25 |
| Greatest diameter of tuber | 55 | 58 | 67 | 69 | 64 | 74 | 69 | 73 |
| Transverse diameter of tuber | 55 | 49 | 41 | 52 | 50 | 50 | 59 | 54 |

feature was used by Hooijer (1966 p. 176) to identify all the East African cuboids with the long-limbed rhinoceros group, and on this basis the Gebel Zelten cuboids would also be identified with the long-limbed rhinoceroses.

TABLE 19

Rhinocerotidae indet. Post-cranial material

Cuboid

| | B.U.22059 | B.U.22060 | M.29308 | M.18892 | M.18890 |
|---|---|---|---|---|---|
| Anterior height | 49 | 43 | 43 | 47 | 45 |
| Anterior width | 44 | 43 | 39 | 44 | 36 |
| Greatest antero-posterior width | 79 | 79 | – | 73 | 63 |

*Navicular.* The three specimens are similar in size but exhibit several contrasting features. B.U.22062 agrees in size with M.25187 from East Africa. The astragalar facet is reduced in the antero-medial corner, giving a facet shaped almost as a right-angled triangle with the right angle postero-laterally. The bone is proximo-distally compressed and has strong antero-medial and postero-lateral tubercles. M.29310 is large and less compressed than B.U.22062. The antero-medial corner is stronger and the astragalar facet is more nearly rectangular. The bone agrees closely with M.18887 from East Africa, which was grouped with the long-limbed rhinoceroses by Hooijer (1966 p. 176). M.29311 is compressed and the bone is produced into two large tubercles in the postero-lateral and postero-medial corners. The distal facet is larger than that of M.29310, and the cuboid and posterior facets are more pronounced in B.U.22061. The strength of the tubercles agrees with features of the metapodials in the short-limbed rhinoceroses, which also carry very strong tubercles, and this suggests that B.U.22061 may belong with the short-limbed rhinoceroses. Reasons for regarding M.29310 as belonging with the long-limbed rhinoceroses are its agreement with the navicular from East Africa (M.18887), and features of the ectocuneiform mentioned below.

*Ectocuneiform.* The ectocuneiforms vary in size, all are deep proximo-distally as in *D. sumatrensis* but in all, as in the East African specimens (Hooijer 1966 p. 177), the postero-medial region is produced much further posteriorly than in *D. sumatrensis* or *R. unicornis.* The distal facet for the Mt.III agrees in M.29312 and B.U.22063 with the proximal facet of B.U.22031, suggesting that these specimens belong with the long-limbed rhinoceroses. The proximal facet of M.29312 also agrees closely with the distal facet of navicular M.29310 with which it can be articulated, which suggests the grouping of the three bones Mt.III (B.U.22031), navicular (M.29310) and ectocuneiform (M.29312).

## CONCLUSION

The rhinoceroses of Gebel Zelten and Moghara belong to the same species, and agree at the generic level with those from the Lower Miocene of Africa south of the Sahara. *Aceratherium campbelli* is similar to *A. acutirostratum,* and derivation from a common ancestor is thought likely to have occurred probably in the late Oligocene.

TABLE 20

Rhinocerotidae indet. Post-cranial material

Navicular

| | M.29310 | B.U.22061 | B.U.22062 | M.25187 | M.18887 | *A. incisivum* | *R. unicornis* | *D. sumatrensis* |
|---|---|---|---|---|---|---|---|---|
| Greatest anterior height | 29 | 26 | 23 | 26 | 31 | 25 | 30 | 21 |
| Total width | 52 | 63 | 51 | 47 | 53 | 46 | 58 | 45 |
| Antero-posterior diameter | 68 | 64 | 62 | 60 | 64 | 58 | 75 | 50 |

TABLE 21

Rhinocerotidae indet. Post-cranial material

Ectocuneiform

| | Gebel Zelten | | | | | E. Africa | | |
|---|---|---|---|---|---|---|---|---|
| | M.29312 | B.U.22065 | B.U.22063 | B.U.22064 | B.U.22066 | M.18905 | M.18886 | *D. sumatrensis* |
| Anterior height | 32 | 26 | 28 | 28 | 31 | 31 | 26 | 27 |
| Anterior width | 54 | 45 | 49 | – | – | 51 | 48 | 46 |
| Antero-posterior diameter | – | 50 | 52 | 52 | 55 | 51 | 52 | 40 |

*Brachypotherium snowi* is similar and probably very closely related to *B. heinzelini* and also resembles the European form *B. brachypus*. *Brachypotherium* first occurs in Europe in the early Miocene, and with reference to brachypotheres Osborn (1900) states :

'they have no known prototypes in the Oligocene of either Europe or America. Either the original home of this type is Africa, and if so they came into Europe with the Mastodons, or they represent an offshoot of the Aceratheriinae.' (Osborn 1900 p. 249.)

Mayet (1908) suggested that *Brachypotherium* represents a new mutation of *Aceratherium*, but Stehlin (1925) disagreed with this. The North and East African material is probably the earliest known of *Brachypotherium* but gives no indication of the ancestry of the group ; however Osborn's suggestion that Africa was the original home of the genus *Brachypotherium* is supported by the presence there of two species in the early Miocene. The European *Brachypotherium* may have entered from Africa in early Miocene times when giraffoids and proboscideans also invaded Europe.

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PLATE 1

***Aceratherium campbelli*** sp. nov.

Fig. 1. Skull M.29250 dorsal view. (Holotype.)
Fig. 2. Skull M.29250 palatal view. (Holotype.)
Fig. 3. Skull M.29250 right lateral view. (Holotype.)

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PLATE 2

***Aceratherium campbelli*** sp. nov.

FIG. 1. Nasals M.29251 left lateral view. × 0·6, approx.

FIG. 2. Nasals M.29251 dorsal view. × 0·6, approx.

FIG. 3. Skull M.29250 occipital region. × 0·3, approx. (Holotype.)

1

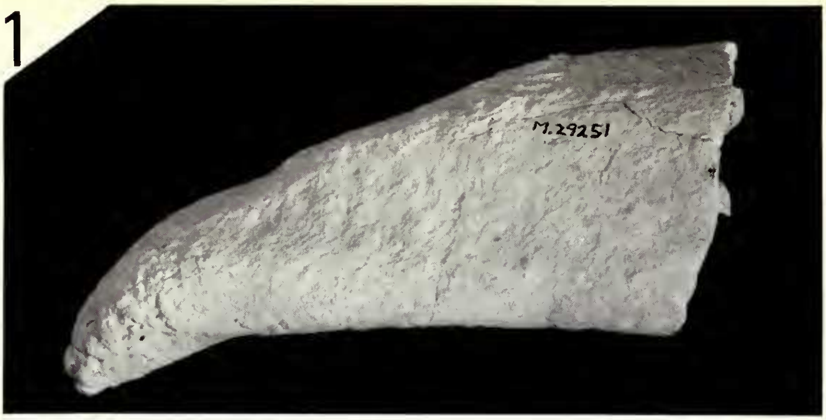


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PLATE 3

***Aceratherium campbelli*** sp. nov.

FIG. 1. Uncollected skull before excavation.

FIG. 2. Uncollected skull after excavation.

N.B. Both figures from colour transparencies which were kindly supplied by Dr R. C. Selley.

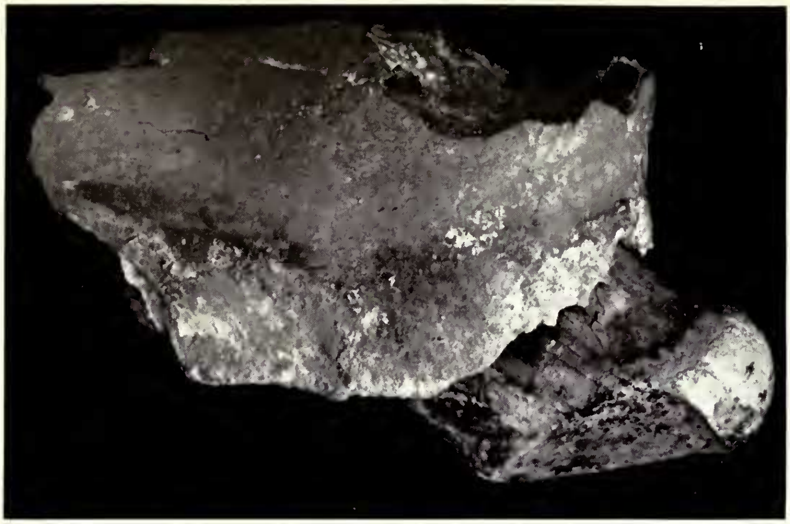
1

2

## PLATE 4

***Aceratherium campbelli*** sp. nov.

FIG. 1. Upper right incisor M.29252 lateral view. × 1, approx.
FIG. 2. $M^2$ lingual fragment M.29256 occlusal view. × 1, approx.
FIG. 3. $M^3$ M.29254 occlusal view. × 1, approx.
FIG. 4. $M_3$ M.29258 occlusal view. × 1, approx.
FIG. 5. $P_4$ M.29257 occlusal view. × 1, approx.
FIG. 6. Upper incisor which may belong with *Aceratherium* M.29266 lingual view. × 1, approx.



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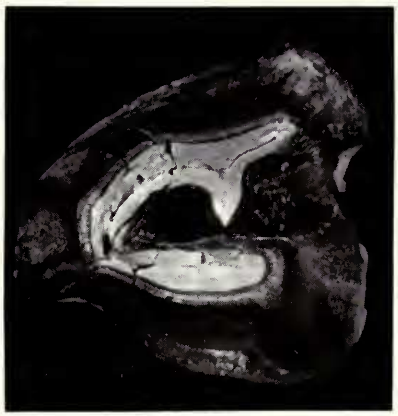

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## PLATE 5

***Aceratherium campbelli*** sp. nov.

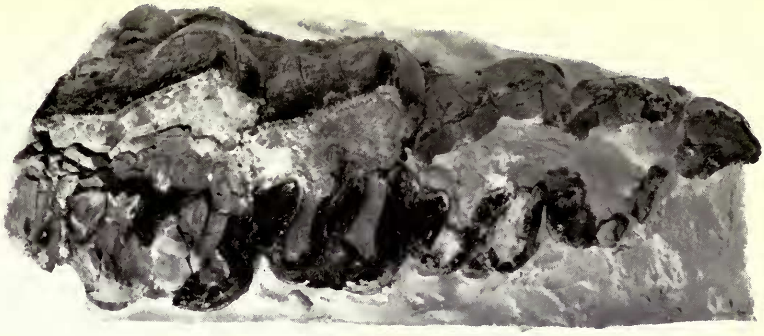
FIG. 1. Upper right cheek teeth M.29252 occlusal view. × 0·7, approx.
FIG. 2. Right second metacarpal B.U.22042 medial view. × 0·5, approx.
FIG. 5. Right fourth metacarpal B.U.22041 anterior view. × 0·6, approx.
FIG. 6. Right fourth metatarsal B.U.22037 anterior view. × 0·5, approx.

***Brachypotherium snowi*** (Fourtau)

FIG. 3. A first incisor M.29265 anterior view. × 0·5, approx.

Rhinocerotidae indet.

FIG. 4. A left calcaneum M.29293 dorsal view. × 0·5, approx.
FIG. 7. A right calcaneum from East Africa M.10364 dorsal view. × 0·5, approx.
FIG. 8. A right calcaneum from East Africa M.10364 medial view. × 0·5, approx.



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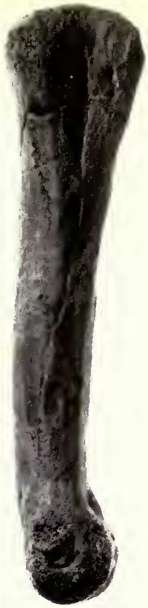

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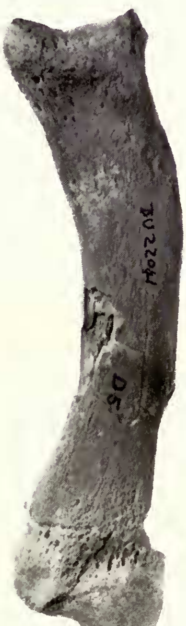

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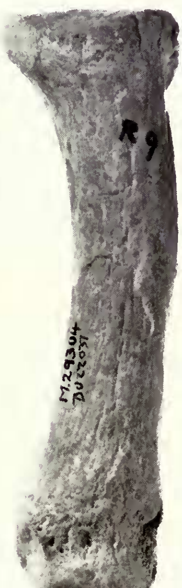

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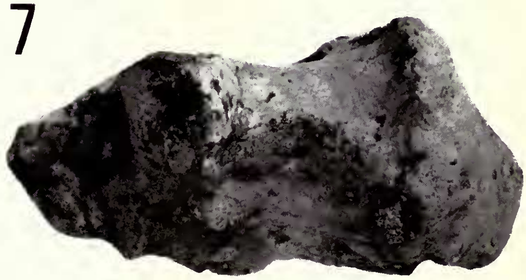

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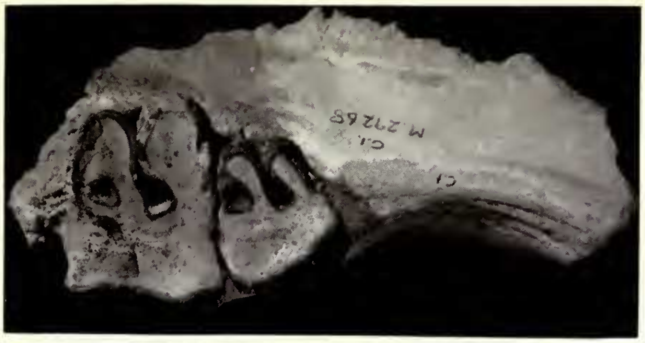
PLATE 6

***Brachypotherium snowi*** (Fourtau)

FIG. 1. Maxillary fragment with $P^2$ and $P^3$ M.29268 occlusal view.
FIG. 2. $M^1$ and $M^2$ M.29269 occlusal view.
FIG. 3. Mandibular symphysis M.29264 dorsal view.
FIG. 4. Right mandibular fragment with $P_3$–$M_1$ M.29260 occlusal view.
FIG. 6. Right $P_3$–$M_1$ M.29260 labial view.
FIG. 5. Left, third metacarpal M.29275 proximal facets.
FIG. 9. Left, third metacarpal M.29275 anterior view.
FIG. 7. Left astragalus M.29279 anterior view.
FIG. 8. A second, lower incisor M.29263 lingual view.

All figures × 0·5, approx.



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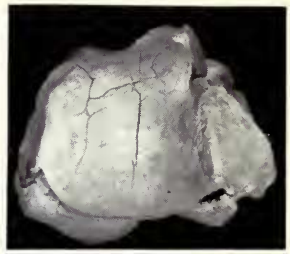

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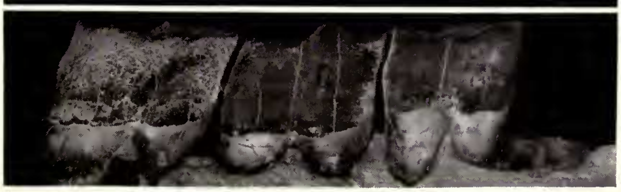

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PLATE 7

***Aceratherium campbelli*** sp. nov.

FIG. 1. A right mandibular fragment with $P_2$–$M_1$ M.29259 occlusal view. × 0·5, approx.

FIG. 2. Right mandibular fragment M.29259 labial view. × 0·5, approx.

***Brachypotherium snowi*** (Fourtau)

FIG. 3. A right mandibular fragment with $D_2$–$D_4$ and $M_1$ M.29262 occlusal view. × 0·5, approx.

FIG. 4. Right mandibular fragment with $D_2$–$D_4$ and $M_1$ M.29262 lateral view. × 0·5, approx.

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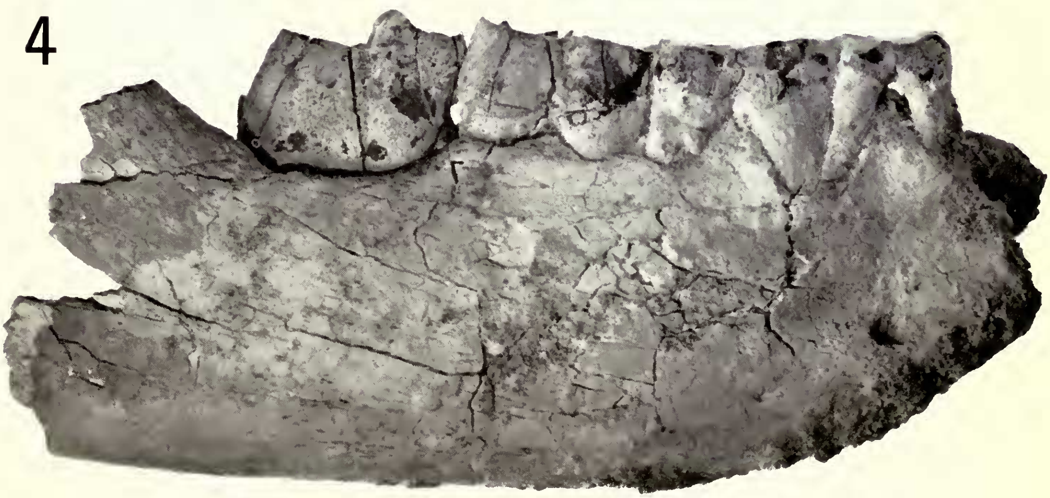

PLATE 8

***Brachypotherium snowi*** (Fourtau)

FIG. 1. Left mandible with $D_1$–$D_4$ erupted B.U.22025 occlusal view. × 0·5, approx.

FIG. 2. Left mandible with $D_1$–$D_4$ B.U.22025 lateral view. × 0·5, approx.

1


2